

The University of Chicago

INTERRELATIONS OF THYROID
AND GONAD IN THE DEVELOPMENT OF
PLUMAGE AND OTHER SEX CHARACTERS
IN BROWN LEGHORN ROOSTERS

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

DEPARTMENT OF ZOÖLOGY
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By
BEN B. BLIVAISS

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BEN B. BLIVAISS²

Whitman Laboratory of Experimental Zoölogy, University of Chicago

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This investigation has been aided by a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago. Preliminary reports were published in the *Ana-*

tomical Record Supplement (Blivaiss and Domm, 1941, 1942, 1944).

Grateful acknowledgment is made to Dr. Erwin Schwenk, of the Schering Corporation, for the alpha-estradiol benzoate (Progynon-B) and the testosterone propionate (Oreton) used in this investigation; and to Mr. I. D. Rotkin for his aid in the feather photography. The crystalline thyroxin was supplied by E. R. Squibb and Sons.

² Present address: Department of Zoölogy and Physiology, University of Illinois, Urbana, Illinois.

I. INTRODUCTION

THE studies of Professor F. R. Lillie and his associates (Lillie, 1942) and those of other investigators (Goodale, 1916; Benoit, 1923*a, b*; M. M. Zawadowsky, 1926) have demonstrated the influence of estrogens on the determination of feather color and form. Domm (1927) showed that the plumage of the Brown Leghorn hen became cocky following sinistral ovariectomy but reverted to the henny type after hypertrophy of the rudimentary right gonad. It was postulated that the reversion to henny plumage was due to secretion of estrogenic hormone by the hypertrophied right gonad; and Gray (1930), who made a careful study of the histology of these gonads in Domm's series, found evidence to support this assumption. Furthermore, removal of the hypertrophied right gonad in such hen-feathered poulards brought about a reversion to cocky plumage, which was permanently retained (Domm, 1927, 1929*a*). Additional evidence in support of the view that estrogenic hormones control the development of henny plumage in the Brown Leghorn was obtained when it was shown that the administration of these substances in roosters, capons, or bilaterally ovariectomized poulards brought about the development of normal female plumage in such individuals (Domm and Gustavson, 1929; Juhn and Gustavson, 1929, 1930; Lillie and Juhn, 1932).

The development of female or female-like plumage has also been reported in males of sexually dimorphic breeds following thyroid feeding (Cole and Reid, 1924; Torrey and Horning, 1925*a, b*; and others; see Schneider, 1939, for an extensive review of the early literature). With thyroid feeding, there was an extension of barbulation in the normally hackled feather areas, an increased deposition of black melanin, and a shortening and

rounding of the feathers. Some investigators have designated these plumage modifications as "feminization" (Torrey and Horning, 1922; Giacomini, 1927), while others have argued the contrary (Greenwood and Blyth, 1929; Zawadowsky and Rochlin, 1928). The lesser amount of black melanin normally present or produced by thyroid feeding in the Brown Leghorn hen, as compared to the rooster, was believed by Torrey and Horning (1925*a*) to result from the secretion of an ovarian substance which nullified the action of the thyroid.

The feeding of large doses of fresh (Giacomini and Taibell, 1927) or desiccated thyroid (B. M. Zawadowsky, 1925*a, b*; and others) to various breeds of fowl resulted in the blanching of feathers and the development of an abnormal feather structure. These feathers were described as "silky and exhibiting a lack of hooks on the barbs" (Martin, 1929).

In cases of hypothyroid anomalies, the feathers are reported to have shown increased hackling and pigment modifications typical of the cocky plumage in a Brown Leghorn hen (Krizeneky, 1927), and a Rhode Island Red pullet (Landaer, 1929), and henny feathering in a Silver Dorking male (Buchanan, 1926).

Development of a "male-like" plumage pattern, due mainly to a decrease in barbulation, accompanied by an increased deposition of reddish-brown pigment, has been reported following thyroidectomy in the adult Brown Leghorn hen (Greenwood and Blyth, 1929; Parkes and Selye, 1937; Greenwood and Chu, 1939). Similar modifications were observed in chick, juvenile, and adult plumages when female Brown Leghorn chicks were thyroidectomized before 10 days of age (Blivaiss and Domm, 1942*b*). Thyroid secretions have been suggested to have a parallel or complementing function to theelin in determination of the

sexually dimorphic plumage pattern (Fraps and Burrows, 1939).

Following thyroidectomy in the Brown Leghorn rooster, Greenwood and Blyth (1929) and Parkes and Selye (1937) reported that some of the plumage became reddish-brown in color and lacy in appearance. The feathers of the breast, cape, saddle, wing bow, and covert exhibited a replacement of the black, red, and yellow melanins, in varying amounts by a reddish-brown pigment, accompanied by a restriction of barbulation. These modifications were not permanent, since normal plumage regenerated after the molt. Similar plumage modifications have been observed following hypophysectomy (J. B. Mitchell, 1929; Hill and Parkes, 1935*a*; Nalbandov and Card, 1943); and Hill and Parkes (1935*b*) reported a restoration to normal in such plumage following thyroxin administration.

In some fowl, thyroid administration in physiological doses was reported to result in an acceleration of gonad activity (Crew, 1925; and others). An inhibitory effect on the endocrine and gametogenic activity of the testis has been reported after thyroidectomy in the White Leghorn (Benoit and Aron, 1934) and in the Brown Leghorn (Greenwood and Chu, 1939).

The limited and often conflicting data available as regards the influence of the thyroid gland in determination of plumage pattern and gonad function in the domestic fowl suggested the need for a further systematic investigation of this problem on a larger number of birds and with a longer period of observation. This study has been concerned with the effect of thyroid removal in young chicks on the immature and mature plumage patterns and on gonad function. The form, color, and growth rate of feathers were studied in thyroidectomized birds and

after treatment with thyroxin and estrogen. The gametogenic and endocrine activity of the gonads was observed, the former by histological study and the latter by observations on modifications in secondary sex characters and behavior before and after treatment with thyroxin, estrogens, and androgens. Questions considered are: (1) What are the relations of the thyroid to body growth and gonad function? (2) What are the characteristics of plumage pattern and growth rate in the absence of the thyroid? (3) What are the functions of the gonadal secretions in the determination of plumage pattern and growth rate in the absence of the thyroid? (4) Are thyroid and gonad secretions necessary for expression of the normal plumage pattern and feather growth rate?

This report is based on data obtained from 98 completely thyroidectomized and 154 incompletely thyroidectomized roosters, operated on or before 10 days of age. Over 50 per cent of these were observed beyond 6 months postoperatively and some until they were 1-2 years old (see Table 1).

II. MATERIALS AND METHODS

The single comb, light brown Leghorn was selected for this investigation because of its extensive use in this and other laboratories for studies on the influence of gonadal and other hormones on the physiology and morphogenesis of growing feathers.

Previous workers, as well as this author, experienced considerable difficulty in obtaining complete thyroidectomy by operation of birds beyond 1 month of age. This was believed to result from the leaving of rests by the developing thyroid along its posterior migratory path (Lillie, 1936). These rests may hypertrophy after removal of the main mass. Thyroidectomy on or before the tenth

day of age was found to be most satisfactory in the production of a complete athyroidic condition. In an effort to alleviate operative shock, removal of the two lobes was performed in separate operations between 6 and 10 days of age.

A description of the anatomy of the thyroid gland area and the procedure for thyroidectomy are omitted, since the essentials have previously been described by Greenwood and Blyth (1929), Schwarz (1930), Greenwood and Chu (1939), and Marvin and Smith (1943). Thyroidectomy was performed on over three hundred birds. The complete removal of the gland was confirmed by macroscopic examination of the thyroid area and the histological examination of all questionable tissue. Further confirmation was usually obtained by scrutinizing plumage modifications.

In order to remove any regenerating thyroid rests in operated birds, biopsies were performed on all questionable cases at intervals of 2-3 months. The number of athyroidic cases was increased by this practice. It was found necessary to keep the thyroidectomized birds at a higher room temperature (75° - 80° F.) than the normals because of their inability to adjust themselves to lower temperatures.

All birds were weighed and combs measured at the time of the operation and at monthly intervals thereafter. When definitely formed feathers appeared, samples of each plumage stage were taken at regular intervals from the various body areas.

For the study of feather growth rates, a modification of the method developed by Juhn, Faulkner, and Gustavson (1931) was employed. Growth rates were studied in the region of the anterior breast, posterior breast, back, and saddle. Twenty-five papillae in five rows of five papillae each were selected and marked in comparable areas of each of

the four feather regions measured. All measurements were made on birds which were at least 6 months of age, at which time the controls were sexually mature. Measurements were made at 2- or 4-day intervals.

Differences between feather growth rates of normal and thyroidectomized birds were examined for statistical significance by making use of comparisons between appropriate groups. The differences were analyzed by "Student's" *t*-test, and the results are here expressed in terms of *P* ("Student," 1925). Values of *P* less than 0.05 are customarily considered significant, whereas values less than 0.01 are very significant.

Testes for histological study were fixed in Bouin's fluid and stained with Harris haematoxylin. The adrenal and pituitary glands have been preserved for further examination.

III. EXPERIMENTAL OBSERVATIONS

A. BODY GROWTH

To understand and interpret better the effects of thyroidectomy on the reproductive system, plumage pattern, and feather growth rate, it seemed advisable to study modifications in body growth. Varying degrees of retardation in body growth have been reported following thyroidectomy in the chicken (Greenwood and Blyth, 1929; Schwarz, 1930; Payne, 1944) and in the duck (Benoit and Aron, 1934). Since thyroidectomy is associated with a hypogonadic condition, one might expect that body growth of such individuals would be similar to that of the capon.

Completely thyroidectomized roosters have a squat, dwarflike appearance when compared with the more erect and larger normal cock (Figs. 1-3). Incompletely thyroidectomized roosters assumed a similar posture but to a lesser extent, de-

pending on the degree of hypothyroidism (Fig. 3).

The hypothyroidic birds at all ages exhibited an unusual subcutaneous obesity in the neck, back, and breast areas and internally about the cardiac, intestinal, gizzard, and rectal areas. The increased obesity probably accounts for a significant proportion of the weight gain in the thyroidectomized roosters.

The average body weight at 6 months of age of a group of seven thyroidectomized roosters, which lived to be at least 1 year old, was 736.6 gm. compared to 1,564.8 gm. for a similar group of nine controls as shown in Figure 21.

The growth curves of normal and thyroidectomized roosters showed an increasing divergence with increasing age. The percentage ratio of thyroidectomized

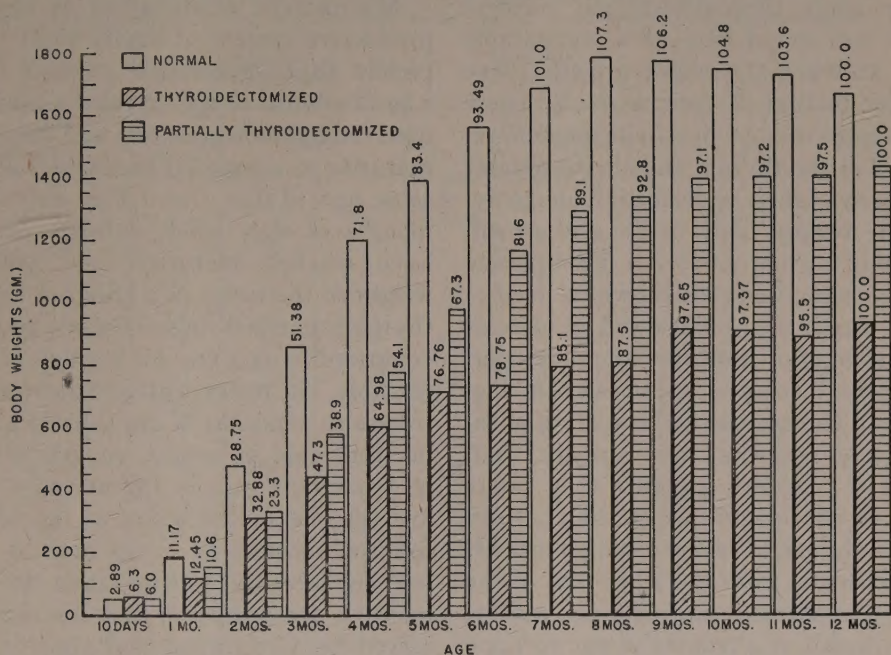


FIG. 21.—Body weights of normal and thyroidectomized roosters. Figures at top of each column are percentages of weight at 12 months of age attained at end of each month.

The skeleton, particularly the main wing and leg bones, and the viscera exhibited a reduction in size compared to controls, which was more conspicuous in the older birds than in the younger ones. The excessive length of the upper beak and of the claws observed in the athyroidic birds is no doubt a result of their infrequent use.

Completely thyroidectomized roosters exhibited a sharp decrease in growth rate, as determined by body weight, when compared with normals of the same age.

to normal body weights decreased from 62.3 per cent at 1 month of age to 47.0 per cent at 6 months. The increase in this ratio to 55.8 per cent at 12 months of age resulted from the continued growth of the thyroidectomized males, while the controls reached their maximum at 6–7 months of age.

The smaller monthly increment in actual grams as well as percentage increase in body weight of the thyroidectomized rooster was not conspicuous in the first 6 months when they were only 78.75 per

cent of their 12 months' weight, compared to 93.5 per cent for the normals (Fig. 21). The athyroidic males did not reach 97 per cent of their 12 months' weight until they were 9 months of age. These data differ from those of Greenwood and Blyth³ (1929) as regards absolute body weight and the character of the growth curve. They reported a 300-400 gm. higher absolute body weight for their adult thyroidectomized roosters than was found here at a comparable age, and a body-weight growth curve similar to that of their normals. These differences may be due to incomplete removal of the thyroid and/or the greater maturity of their birds at thyroidectomy.

The average body weight and growth curve of a group of eleven incompletely thyroidectomized roosters which lived to be at least 1 year old showed an increasing divergence from the complete operates with increasing age, as seen in Figure 21. Though the body weights of incomplete operates were greater than those of complete operates, they rarely reached the magnitude of the controls. The body weight of the incomplete operates changed from 129.7 per cent of the complete operates and 65.6 per cent of the normals at 4 months of age to 155.9 per cent of the complete operates and 87.1 per cent of the normals at 12 months of age. The increase in the percentage ratio of body weight of incomplete operates to normals with increasing age indicates the closer approach of the former to the normal absolute size and body-weight growth curve at maturity.

B. REPRODUCTIVE SYSTEM

A reduction in growth of the reproductive system and of gonad activity has been reported following thyroidectomy in mammals (Smelser, 1934; Zalesky and

Wells, 1937). The reduced growth of head furnishings observed in thyroidectomized roosters (Figs. 1-3) suggests an inhibition of gonad activity, and this is confirmed by data from autopsies of such birds. Benoit and Aron (1934) and Greenwood and Chu (1939) reported a reduction in testis size and an absence of spermatozoa in thyroidectomized roosters for limited periods.

Macroscopic examination of the reproductive system of ninety-eight completely thyroidectomized roosters from 1 to 22 months of age revealed a conspicuous reduction in gross size and degree of maturity as compared to normals of the same age (Table 1 and Fig. 22). At 6 months of age, when normal roosters have reached maturity, the average weight of the testes in a group of twelve thyroidectomized roosters was 0.30 gm., compared to 14.3 gm. for a group of five controls. The testes of athyroidic roosters from 2 to 7 months of age showed a 67.8 per cent gain in weight, compared to a 98.3 per cent gain in the normals. The average size of the testes in thyroidectomized roosters at 12-22 months was not significantly greater than at 6-7 months. The reduction in testis size observed by Greenwood and Chu (1939) was less than that observed in these experiments.

In adult completely thyroidectomized roosters, the vas deferens was thin and straight, and semen could rarely be expressed from it. In normals, at 18-20 weeks of age the ductus deferens is coiled and shows an increasing diameter due to the accumulation of sperm-filled semen. The ductus deferens of thyroidectomized roosters remained relatively thin and exhibited only slight coiling even as late as 18-22 months of age. The reproductive system of these older athyroidic roosters had the appearance typical of a 2- to 3-months-old control. No other investi-

³ This is the only previous study to provide sufficient data for comparison.

gators are known to have made any observations on the appearance of the ductus deferens in such individuals.

The lack of coiling and increase in diameter of the vas deferens of athyroidic roosters may be related to a reduction or absence of semen production. However, since growth of the vas deferens is de-

spermatozoa at 18-20 weeks of age. The thyroidectomized males exhibited secondary spermatocytes at 22-24 weeks but did not show any spermatozoa even as late as 12-22 months of age. The tubular epithelium of the testes of thyroidectomized roosters remained relatively "cuboidal," in contrast to its more

TABLE 1

TESTIS WEIGHTS OF NORMAL AND THYROIDECTOMIZED ROOSTERS

AGE (MONTHS)	COMPLETE THYROIDECTOMY			INCOMPLETE THYROIDECTOMY			NORMAL		
	No. of Cases Au- topsied	Testes		No. of Cases Au- topsied	Testes		No. of Cases Au- topsied	Testes	
		No. of Cases	Gm.		No. of Cases	Gm.		No. of Cases	Gm.
1.....	8			5					
2.....	12	2	0.16	18			6	6	0.2
3.....	8	5	0.15	16			6	6	2.6
4.....	15	11	0.19	19	8	0.3	5	5	4.9
5.....	5	3	0.09	14	4	1.2	5	5	8.2
6.....	13	12	0.30	10	5	3.1	5	5	14.3
7.....	10	5	0.49	21	7	5.8	5	5	14.4
8.....	8	3	0.44	13	6	8.5	5	5	10.1
9.....	4	1	0.53	11	2	13.5			
10.....	6	1	0.30	9	5	9.7	5	5	13.2
11.....	2	1	0.24	3	2	2.9			
12.....	3			8	2	14.2	5	5	15.5
13.....				1					
14.....				3					
15.....				1					
17.....	1			1					
18.....	1								
19.....				1					
20.....	1								
22.....	1								
Total.....	98	44		154	41		47	47	

pendent on testis hormone (Domm, 1939), its reduced size may also result from the decreased secretion and utilization of androgens.

Microscopic examination of the testes of athyroidic roosters revealed no significant histological modifications until they were 18-20 weeks old, whereas controls showed signs of spermatogenetic activity at 9-11 weeks (Figs. 4-6). The testes of normal males began to develop secondary spermatocytes at 14-18 weeks and

"columnar" appearance in the normal. The mitotic activity of these cells was sharply decreased in thyroidectomized males, as compared to normals at all ages. The testes of the former had a more compact appearance and a smaller seminiferous tubule and lumen than controls, and in many cases the tubules had practically no lumen. This condition was also noted by Greenwood and Chu (1939). The interstitial cells were more conspicuous in the testes of thyroidectomized

roosters than in normals, which may be due in part to the smaller size of the tubules in the former. In this respect they resembled the normal during a period of its early development.

The incompletely thyroidectomized roosters exhibited varying degrees of increased testicular development when compared with completely thyroidectomized individuals. The testes of such roosters were larger than those of complete operates, though generally much

smaller than normal, as shown in Table 1. The testes generally revealed a delay in spermatogenetic activity, as compared to controls, but a sharp increase over the complete operates. Some incomplete operates showed secondary spermatocyte at 14–16 weeks of age and spermatozoa at 23–25 weeks of age, which is within the normal range. However, some of these did not develop spermatozoa until 10–12 months of age. The marked delay in sexual maturation of incomplete operates

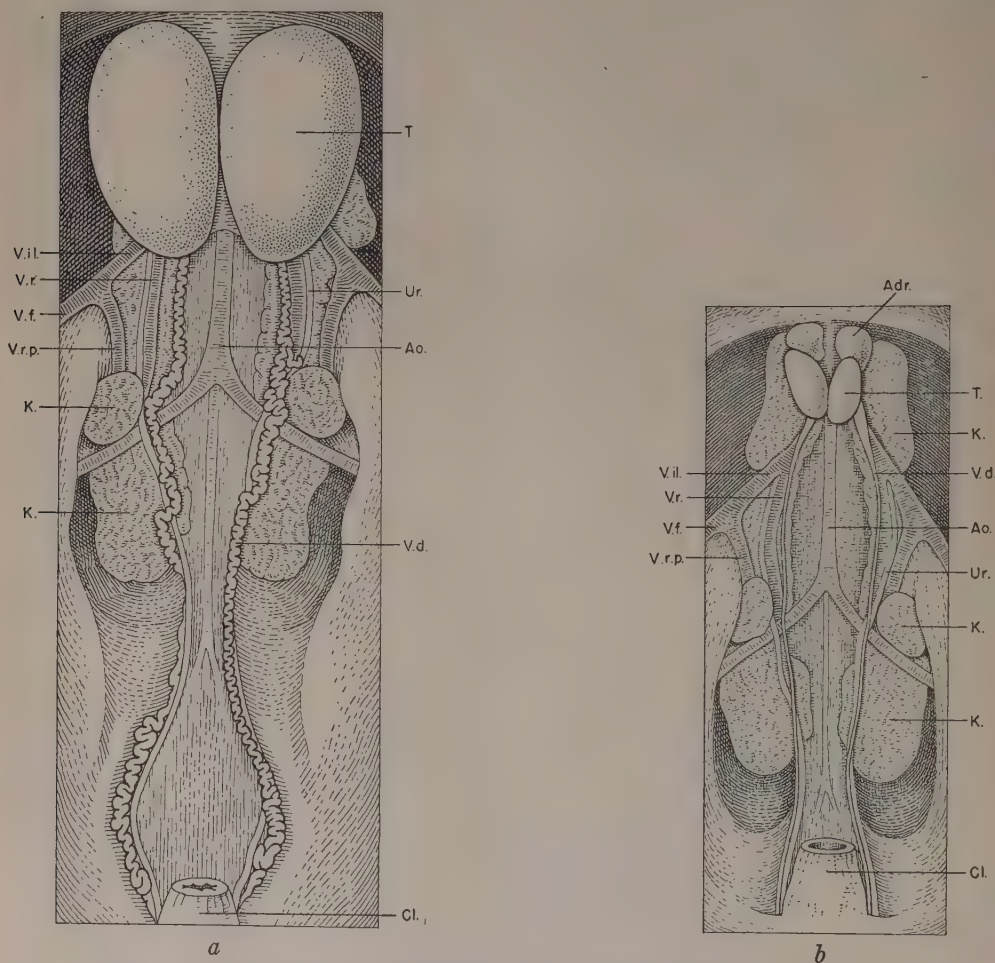


FIG. 22.—*a*, normal rooster; *b*, thyroidectomized rooster. Drawings of primary and accessory organs of reproduction of normal and thyroidectomized roosters at 7 months of age. *Adr.*, adrenal; *Ao.*, aorta; *Cl.*, cloaca; *K.*, kidney; *T.*, testes; *Ur.*, ureter; *V.d.*, vas deferens; *V.f.*, femoral vein; *V.il.*, iliac vein; *V.r.*, renal vein; *V.r.p.*, renal portal vein. Drawn to scale.

indicates that complete thyroidectomy is not necessary for inhibition of spermatogenesis or testis growth.

The ductus deferens of incompletely thyroidectomized roosters exhibited varying degrees of development from that typical of athyroidic individuals to one similar to normal. With increasing age, especially beginning at 5-6 months, the ductus deferens of incomplete operators showed an increase in diameter and coiling due to semen accumulation. However, in some, the vas deferens remained relatively straight and of small diameter, typical of the juvenile condition, until 9-12 months of age.

C. HEAD FURNISHINGS

Comb growth is known to be controlled by testis secretions, as indicated by its atrophy following gonadectomy and its hypertrophy after androgen administration. Since the testes revealed an inhibition of growth in thyroidectomized roosters, we were interested in determining to what extent this condition modified growth of the comb. A reduced growth rate and a subnormal adult size have been reported for the comb of cocks and pullets for a period of 1-4 months after thyroidectomy (Schwarz, 1930; Benoit and Aron, 1934; Greenwood and Chu, 1939; Payne, 1944). However, no data are available for size or growth curve of the comb in adult athyroidic roosters.

I. THYROIDECTOMIZED ROOSTERS

The head furnishings (comb and wattles) of normal roosters become markedly enlarged and red and turgid with development of the testes. While the head furnishings of thyroidectomized roosters in these experiments exhibited an increase in size and vascularity with increasing age, they were, nevertheless, considerably smaller than normal at all ages ob-

served (Figs. 1-3). At 4 months of age the average comb size of a group of seven thyroidectomized males, which lived to be at least 1 year old, was 27.4⁴ per cent of the comb size of a similar group of nine controls but was reduced to 18.3 per cent of the controls at 12 months, as seen in Figure 23.

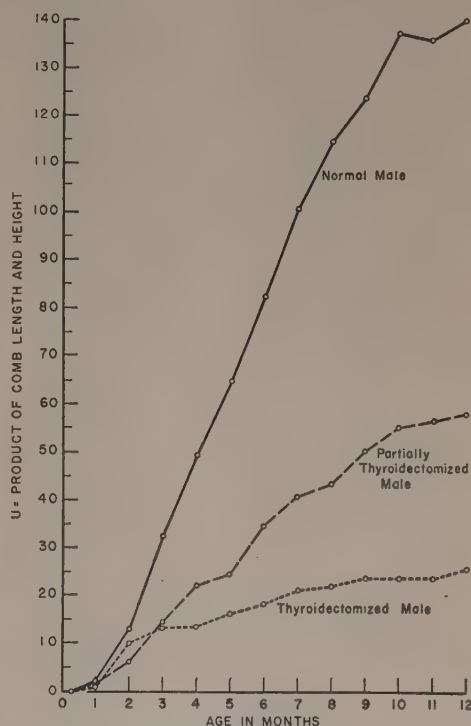


FIG. 23.—Comb size of normal and thyroidectomized males.

After 2 months of age the percentage ratio of the comb size of thyroidectomized males to the size of the normals exhibited a progressive decrease. The reduction in this ratio after 2 months of age is correlated with increased gonad activity in normals, which results in a rapid growth of the comb.

There was a distinct difference in

⁴ Based on the product of comb length and height which has been found to have the closest correlation with comb weight (Jones and Lamoireux, 1943).

comb growth rates between thyroidectomized and normal roosters. Until 9 months of age, athyroidic roosters had attained a greater percentage of their 12-month size than had the controls (Fig. 23). The largest percentage of comb growth increments was exhibited by the thyroidectomized males during the first to third months. The percentage increments of the normals were smaller but spread over a longer period, from the second to the eighth months.

The average comb size of a group of eleven incompletely thyroidectomized roosters was larger than complete operates but smaller than normals at comparable ages, as shown in Figure 23. In some cases the comb size was only slightly larger than that of the complete operates. The difference in comb size between the complete and the incomplete operates became greater with increasing age, especially after 6–8 months of age, when the testes of the latter began to show a sharp increase in size and gametogenic activity. At 12 months of age the comb of the incompletely thyroidectomized roosters was 225.9 per cent of the athyroidic individuals, compared to 41.4 per cent of the controls. The similarity in the comb growth curve of the incomplete operates and normals was shown by the constancy of their ratio of comb size after 5–6 months of age and the similarity of their percentage of 12-month size increments.

2. HORMONE THERAPY

The androgens (Domm, 1927; Gallagher and Koch, 1929) and thyroid secretions (Crew, 1925; and others) have been shown to have a growth-stimulating effect on head furnishings in normal fowl, while estrogens were found to have none (Domm and Gustavson, 1929). Since thyroid secretions exercise a growth-stimulating effect on the comb, it was judged

important to investigate whether the athyroidic condition affects the comb response to injections of thyroxin or steroid hormones.

a) *Thyroid hormone*.—Following thyroxin administration in thyroidectomized roosters, there was an increase in the size and vascularity of the comb. Within 4–6 days after the administration of 0.1 mg. thyroxin, the comb attained a 4.0–5.3 U.⁵ increase in size. The increase persisted for 18–20 days after the injection. With the administration of a larger dose, as four doses of 0.1 mg. or of 0.15 mg. at 6-day intervals, the comb revealed growth within 2–4 days. There was a growth of 6.4–9.3 U. at 12 days after the first injection. A total increase in comb size of 14.0–14.6 U. was attained at 6–8 days after the last injection. The increased comb size was discernible until 26–30 days after cessation of medication. With an alternate-day injection of 0.05 mg. thyroxin for 30 days, which provided a more constant and longer period of medication, there was a 14.6 U. increase in comb size at 4–6 days after the last injection. An increase was revealed within 4 days after the first injection and persisted for over 30 days after the last injection. Biopsies for examination of gonads were omitted on these birds, so as not to interfere with the recording of other observations. The degree of comb response was proportional to the dose administered. Comb growth was also reported by Greenwood and Chu (1939) after feeding desiccated thyroid to thyroidectomized hens.

b) *Estrogenic hormone*.—Administration of alpha-estradiol benzoate in thyroidectomized roosters was generally followed by a decrease in the size and vascularity of head furnishings. With the daily administration of 5.0 γ of estradiol per 100 gm. body weight for 7 days (total

⁵ Based on product of comb length and height.

daily dose, 0.059 mg.), there was a 3.6 U. decrease in comb size within 20 days after the start of injections. A reduction in comb size was evident within 4-6 days after the first injection with this and higher doses. The comb showed no increase in size until 20 days after the last injection. With a daily dose of 10.0 γ per 100 gm. body weight for 20 days (total daily dose, 0.109 mg.), a decrease of 4.6 U. occurred within 24 days. A maximum decrease of 7.6 U. was attained at 33 days after the first injection. The comb showed no increase in size for over 25 days after cessation of medication. At the termination of the daily administration of 16.5 γ per 100 gm. body weight for 22 days (total daily dose, 0.199 mg.), there was an 8.6 U. decrease in comb size. A maximum decrease of 14.9 U., attained at 36 days after start of treatment, persisted for over 30 days after its cessation.

No previous record was found of the effects of estrogens on comb growth or testis activity in thyroidectomized roosters. The decreased comb size observed in such individuals after estradiol administration corresponds to a similar effect observed in cockerels by Hoskins and Koch (1939). This may result from a pituitary gonadotropic inhibition, which would retard androgen secretion. Such an inhibition was reported following administration of estrogens by Moore and Price (1932) in mammals. The decrease in comb size observed in my experiments would therefore indicate that there is no cessation of secretion of the pituitary gonadotropic principle after thyroidectomy.

c) *Androgenic hormone*.—Within 7 days after beginning the daily administration of 1.0 mg. testosterone propionate for 5 days in a 2,660-gm. capon, there was a 15.4 U. increase in comb size. The same medication in a 1,200-gm. thyroidectomized rooster was followed by a 2.2

U. increase in comb size in 7-days. When this was followed by the daily administration of 2.0 mg. testosterone for 8 days, there was a further increase of 12.9 U., to make a total growth of 15.1 U. With the subsequent injection of 3.0 mg. for 5 days to this rooster, the comb revealed an additional growth of 4.1 U. for a total increase of 19.2 U.

The thyroidectomized rooster does not appear able to respond so quickly or so greatly to testosterone propionate medication as does the capon. Greenwood and Chu (1939), after treatment of thyroidectomized hens with a male sex hormone preparation, reported that "there had been no loss of sensitivity in the comb as a result of the removal of the thyroid glands." However, they do not present control data for comparison.

The influence of thyroid secretions in utilization of androgens is demonstrated by a comparison of the effects of individual and combined injections of thyroxin and testosterone propionate. When an athyroidic rooster received 0.5 mg. thyroxin at 3-day intervals and 1.0 mg. testosterone daily, there was a comb growth of 9.2 U. within 7 days. Continuation of the same treatment for another 7 days resulted in an additional increase of 10.3 U., for a total of 19.5 U. Another such individual receiving only the thyroxin medication revealed an increase of 12.9 U. An athyroidic male injected with only the testosterone showed a growth of 3.6 U. In a group of three capons, one was given 0.2 mg. every third day, the second 1 mg. of testosterone propionate daily, and the third both the thyroxin and the testosterone in the same dose. At 6 days after start of medication, the comb of the first had grown 0.4 U., the second 19.4 U., and the third 22.9 U. After 18 days of medication, the comb of the first showed no further increase, the second revealed a total growth of 52.7 U., and the third a

growth of 56.6 U. Thyroxin appears to increase the utilization of testosterone or has a synergistic effect with it on comb growth.

D. SPURS

It has been observed that spur growth in the capon exceeds that of the normal male, and, as a consequence, it is assumed that the testis secretion exercises a certain degree of inhibition on spur growth in the rooster (Domm, 1927). The hypogonadic condition of athyroidic roosters might therefore be expected to favor spur growth unless other factors, such as those associated with thyroid function, are involved. As far as the author is aware, no previous study has been made of spur development of chicks after thyroidectomy.

In the thyroidectomized rooster the spurs were "knoblike" and showed relatively little growth. They generally measured less than 1 mm. in length until the chicks were 7 or 8 months of age. The spurs of the normal rooster increased from a length of 1-2 mm. at 2 months to 9-10 mm. at 7 or 8 months of age. At 1-2 years the spurs of thyroidectomized roosters may grow to a range of 2-7 mm., compared to a range of 11-15 mm. in the normal. As also noted by Caridroit and Regnier (1944), the spurs became detached from the metatarsal bone and movable in the adult. The central part was composed of fibrous connective tissue instead of being calcified.

In the incompletely thyroidectomized rooster the spurs showed approximately the same size as in complete operates until 4-5 months of age. After this time the spurs of incompletes grew faster than in completely thyroidectomized roosters. The spurs of some incomplete operates measured 1 mm. in length at 7 months, while others measured 8-11 mm. and reached 16-19 mm. at 12 months. These

variations were probably due to differences in the size of the remaining thyroid fragments.

From these results it would seem that the thyroid must be taken into account in any consideration of factors regulating or controlling spur growth and calcification.

E. BEHAVIOR

The characteristic pugnacity, crowing, and aggressive sexual behavior of the rooster is not revealed by the capon. The initiation and maintenance of aggressiveness and male mating behavior have been shown to be dependent on androgens (Domm, 1927; Allee, Collias, and Lutherman, 1939; Davis and Domm, 1941). Consequently, observations were made to determine whether the inhibition of gonad development in thyroidectomized roosters modified their mating behavior and if the athyroidic condition had any influence on their activities.

Though the capon is generally negative in its sexual behavior, it does not have the conspicuous lethargy characteristic of thyroidectomized roosters. Athyroidic individuals show a sharp decrease in activity when compared with controls. They generally have a droopy appearance and assume a squatty, rather than the characteristic upright, posture of normals. A similar lethargy was observed by Greenwood and Chu (1939) in their thyroidectomized fowl and by Nalbandov and Card (1943) after hypophysectomy. Completely thyroidectomized fowl stood or sat in their cages with their heads hanging or placed under their wings. Incomplete thyroidectomies generally assumed a more upright posture similar to normals (Figs. 1-3). Both groups manifested the usual excitability at feeding time.

Fighting and pecking in the cages was usually occasioned by the presence of

larger, incompletely operated birds, which would attack the smaller ones. In cages containing similar-sized thyroidectomized birds, relatively little fighting or pecking was observed. The incompletely thyroidectomized birds were more active than the complete operates, especially as regards fighting and pecking in their groups.

At 9-11 months of age some of the thyroidectomized roosters showed a slight strut, but rarely any courtship when tested.⁶ No crowing was observed. Some incomplete thyroidectomies were observed not to have the typical courtship of normal roosters, such as chase, waltz, and circle, or treading of the female, which were revealed by other partial operates. Greenwood and Blyth (1929) and Schwarz (1930) reported treading by presumably incompletely thyroidectomized roosters. They report no observations on crowing. Simmons (1943) reported that a cockerel thyroidectomized at 5 days of age had not acquired the ability to crow when 82 days old.

Following injection of thyroxin or testosterone propionate, thyroidectomized roosters became more aggressive and belligerent. A similar effect was observed by Allee, Collias, and Lutherman (1939) after androgen medication of normal pullets and hens. After testosterone medication they would strut and waltz about a hen but showed no attempt to mount. No crowing was observed. Courtship, crowing, and treading can be induced by a similar dose of testosterone in normal capons (Domm, Davis, and Blivaiss, 1942). The administration of alpha-estradiol benzoate was observed not to have an effect on the behavior of athyroidic roosters, though larger doses were reported to have induced courtship

and treading behavior in capons (Domm, Davis, and Blivaiss, 1942).

F. FEATHER PATTERN (COLOR AND FORM)

1. PLUMAGE OF NORMAL MALE

Since the plumage of the Brown Leghorn is known from previous descriptions, a detailed account of its characteristics will not be presented; however, a brief survey of pertinent features will be helpful. The plumage of the male passes through four distinct stages, designated as "down," "chick," "juvenile," and "adult." These stages do not appear as sudden or abrupt changes but rather as gradual transformations, resulting from a slow continuous molt during the growth of the bird. While the down and chick plumages are quite similar in both sexes, the later stages are conspicuously different. The characteristic sexually dimorphic plumage does not become pronounced until the juvenile plumage appears.

A detailed description of the normal plumage of the Brown Leghorn may be obtained by consulting Domm (1927), Greenwood and Blyth (1929), or the American Standard of Perfection (1938).

2. PLUMAGE OF THYROIDECTOMIZED MALE

Thyroidectomy was observed to be followed by a replacement of the normal black, brown, red, and yellow melanins⁷ by a light reddish-brown pigment (referred to as "tawny" by Ridgway, 1912) in all plumage stages, accompanied by a decrease in the number of barbules. These modifications resulted in a loss of the characteristic plumage pattern. Most of the feathers of thyroidectomized males

⁶ This involved introducing a rooster that had been in isolation into a pen with a receptive hen.

⁷ Melanin refers to the amorphous black, brown, red, and yellow pigments believed to be formed by oxidation of tyrosine or 3,4-dioxyphenylalanine (Bodansky, 1938).

were entirely reddish-brown in color, noticeably elongated, narrow, tapered, and lacy,⁸ and showed little or no web. The changes in feather form result from an elongation of the feather, a decrease in barbulation, an absence of hooks on barbules, and the abnormal position of some barbules, which lie nearly parallel to the barbs instead of extending laterally. The author found no previous reference to the latter condition in thyroidectomized roosters. These modifications interfered with web formation (Figs. 7-12).

The inhibition of molting in the thyroidectomized rooster was prominent and often resulted in the retention for periods much beyond the normal of a mixture of chick and juvenile feathers in juvenile birds and of juvenile and adult feathers in adult birds. At a time when normal birds have a complete adult plumage, thyroidectomized birds still conspicuously displayed juvenile feathers. The appearance of the adult plumage in thyroidectomized birds was usually hastened by plucking of the juvenile plumage. Operated birds kept in isolation frequently showed a nearly complete juvenile plumage at the time of normal adulthood. The lower feather growth rates of thyroidectomized roosters (see Table 2) also contributed to the delay in assumption of the adult plumage. The contrast between successive feather stages was not so marked in thyroidectomized individuals as in normals, owing to the greater similarity of feathers in the former.

The down and chick feathers which regenerated in areas plucked at the time of thyroidectomy showed evidence of hypothyroidism, both as to color and as to form. In all feather areas of the thyroidectomized cockerel there was either a

complete loss or a partial replacement of the normal pigmentation by a reddish-brown pigment and a decrease in barbulation.

In the adult thyroidectomized rooster operated on or before 10 days of age, body areas normally bearing black webbed feathers demonstrated the modifications in form and pigmentation most conspicuously (Figs. 7-10). Normally hackled or fringed feathers showed a further reduction or even complete loss of web (Figs. 8-9).

The normally black, solid-webbed breast feathers became entirely reddish-brown in color and narrow, elongated, and lacy. The web of the vane may be quite slender and confined to a thin strip along the rhachis or completely absent. The proportion of vane to fluff is greatly increased in feathers of thyroidectomized fowl, as compared to the normal. The fluff formed about one-third to one-quarter of the feather length rather than about one-half, as in controls. This was most conspicuous in the breast plumage. The body fluff, down, and shank feathers showed similar modifications.

The neck hackle exhibited a complete loss of the dark-brown or black pigment in the web. The orange-red of the fringe was blended into a reddish-brown, which extended to the rhachis. These feathers became nearly flufflike in form, owing to the extreme reduction or complete loss of barbulation (Fig. 8). Other hackled feathers with black and brown pigments, such as back, saddle, and wing-bow, showed the same type of modification. Some of the posterior saddle feathers became extremely elongated, approaching the length of the greater tail sickles of the normal rooster. Such feathers revealed virtually no barbulation and were entirely red-brown in color, similar to the other saddle feathers of athyroidic males.

The wing front feathers exhibited a

⁸ The terms "lacy," "fringed," or "hackled" refer to the absence of barbules on barbs so as to form an area of free bristles.

TABLE 2
AVERAGE FEATHER-GROWTH MEASUREMENTS
(In Mm.)

FEATHER AGE (DAYS)	2 NORMAL ROOSTERS				2 CAPONS				2 BILATERAL POULARDS			
	Post. Br.	Ant. Br.	Back	Saddle	Post. Br.	Ant. Br.	Back	Saddle	Post. Br.	Ant. Br.	Back	Saddle
Length												
16.....	13.2	11.5	9.2	9.6	11.6	9.4	7.1	8.6	13.3	11.9	11.0	7.6
24.....	33.1	30.7	24.6	22.3	33.7	30.1	22.3	21.4	34.4	31.2	30.0	22.1
36.....	60.9	56.6	52.6	43.4	64.8	57.4	51.3	44.2	64.1	57.6	57.0	50.0
48.....	83.0	74.4	75.7	63.9	92.8	79.6	76.7	67.6	86.5	74.4	75.0	78.5
60.....	94.9	79.4	85.4	85.4					87.3	78.2	80.5	103.8
80.....	100.8			118.6								
2-Day Growth Increments												
12-24.....	4.7	4.2	3.4	3.2	5.0	4.5	3.2	3.1	4.8	4.3	4.1	3.2
14-24.....									5.1	4.6	4.5	3.4
24-36.....	4.6	4.3	4.5	3.5	5.2	4.5	4.8	3.8	4.9	4.4	4.5	4.6
36-48.....	3.7	2.9	3.8	3.4	4.7	3.7	4.2	3.9	3.7	2.8	3.0	4.7
48-60.....	1.9	0.8	1.7	3.6					1.8	0.6	0.9	4.2

FEATHER AGE (DAYS)	THYROIDECTOMIZED ROOSTERS							
	4 Completes				3 Incompletes			
	Post. Br.	Ant. Br.	Back	Saddle	Post. Br.	Ant. Br.	Back	Saddle
Length								
16.....	2.7	1.6	1.7	3.2	2.5	1.9	2.5	3.6
24.....	9.6	5.5	6.1	9.4	10.0	8.1	8.4	10.2
36.....	22.4	16.7	17.1	20.9	24.7	22.3	22.6	24.4
48.....	34.1	28.0	28.5	31.8	39.8	37.3	36.2	38.9
60.....	45.8	38.1	39.8	41.9	54.3	51.8	50.0	53.6
72.....	56.4	46.2	50.7	51.8	67.6	63.5	62.9	68.1
80.....	63.1	51.1	57.2	58.9	75.6	68.5	69.5	77.4
2-Day Growth Increments								
14-24.....	1.62	0.97	1.0	1.44	1.7	1.4	1.4	1.3
24-36.....	2.13	1.86	1.85	1.92	2.4	2.3	2.3	2.3
36-48.....	1.95	1.88	1.88	1.82	2.5	2.5	2.2	2.4
48-60.....	1.93	1.88	1.88	1.68	2.4	2.4	2.3	2.4

loss of their black melanin and solid webbed vane, becoming reddish-brown in color and lacy in appearance. Wing coverts showed a loss of black melanin, which was replaced by a reddish-brown pigment and a tendency to become narrow and pointed. The vane was a uniform reddish-brown in color, narrow, and had a pointed apex. The web, though not fringed or lacy, was frayed and not well formed on its edges.

The primary flight feathers became narrower (Fig. 11). They displayed a replacement of the normal black melanin by an increased deposition of tan or reddish-brown pigment to form a band of reddish-brown pigment twofold or threefold wider than normal on the edge of the outer vane. A further slight deposition of reddish-brown pigment to form a band 2-3 mm. in width was observed on the edge of the inner vane. The secondaries were slightly narrower and more pointed than normal (Fig. 12). There was a conspicuous increase in the deposition of reddish-brown pigment, which replaced the normal black pigment. The entire outer vane assumed a reddish-brown color, instead of only a band of a quarter to a third of its width, as in the normal. The edge of the inner vane, which is normally entirely black, became reddish-brown in color. In the more medial secondaries, the entire inner vane also assumed a reddish-brown color. This type of modification in the flight feathers was also noted by Greenwood and Blyth (1929). The web of the secondaries, though not fringed or lacy, was not so well formed as in the normal, being frayed on its edges.

The normally broad-webbed tail coverts became markedly slender and tapered. The sickles displayed a narrower web and were considerably shortened in length. Both revealed a replacement of black melanin by a scattered deposition

of reddish-brown pigment, especially at the margins and base of the vane. A decrease in barbulation was usually limited to the base of the vane.

The incompletely thyroidectomized roosters exhibited various gradations in modifications of plumage from the normal to those typical of complete thyroidectomy. They may be divided into two groups as to degree of modification. Group I included those which manifested, throughout, nearly all the pigment changes typical of complete thyroidectomy but not so extensive a degree of decreased barbulation. The feathers of Group I birds displayed characteristics similar to those described by Greenwood and Blyth (1929), Parkes and Selye (1937), and Fraps and Burrows (1939) following thyroidectomy, and by Hill and Parkes (1935a) and Nalbandov and Card (1943) following hypophysectomy. Group II included those which sporadically revealed the pigment and barbulation modifications typical of complete thyroidectomy in a section of some of the feathers, thus indicating a temporary athyroidic condition. The fluctuations in pigmentation and barbulation followed removal of thyroid rests by repeated operations.

In both groups of incompletely thyroidectomized cockerels, the more advanced development of the plumage compared to athyroidic cockerels was conspicuous. The modifications observed were generally similar to those in the adult. The changes in pigment were not so conspicuous here as in the adult, since the juvenile plumage normally has more reddish-brown pigment than the latter. The juvenile modifications will be described with those of the adult, in view of their similarity.

The breast feathers of Group I incompletely thyroidectomized roosters showed a nearly complete replacement of the

black melanin by reddish-brown pigment, but the decrease in barbulation usually was limited only to the edge of the vane. Their shape and form, therefore, were similar to the normal. The apex of these feathers frequently showed a small patch of black melanin, which was larger in the posterior than in the anterior breast feathers. The body down, fluff, and shank feathers exhibited similar pigment changes, but no further significant reduction in barbulation. The reddish-brown pigment which replaced the black melanin was darker in these cases than in completely thyroidectomized fowl. The basal fluff portion of the vane was slate or black in color, similar to the normal.

The neck hackle generally revealed a loss of the dark-brown or black pigment of the web, the entire feather becoming reddish-brown in color. There was no significant decrease in the width of the web or vane, which normally is quite narrow, or a change in the orientation of the barbs. The other hackled dorsal feathers, such as the back and saddle, showed a slight reduction in barbulation. The replacement of their black and red melamins by reddish-brown pigment was extensive but not complete.

The wing front, wing-bow, and wing coverts revealed a loss of black melanin which was replaced by reddish-brown pigment. However, there was no significant decrease in barbulation, the web remaining well formed. The primary flights were black with traces of tan on the edges of the outer vane, while the secondary flights showed only a slight increase in the width of the reddish-brown band on the edge of the outer vane. The remainder of the vane in the latter was black and had a well-formed web.

Tail coverts and sickles revealed no modification of their normal black pigment or barbulation. However, both had

a narrower vane and were shorter than normal.

In Group II incompletely thyroidectomized roosters, the modifications generally appeared only in transverse segments of the feather rather than throughout, as in Group I. The breast revealed a loss of black melanin in varying amounts, which was more extensive in the anterior than in the posterior breast feathers. No significant modifications were observed in many of the feather areas. The maximum degree of modification was usually observed in the feathers regenerating after a biopsy, in which thyroid tissue was removed. In individual feathers a greater degree of modification was generally manifested on the edge of the vane than medially. This results from the fact that the apex of the barb has a higher threshold for hormonal modification than the base (Lillie and Juhn, 1932).

In cases in which the athyroidic condition had prevailed for a considerable period, the entire plumage was reddish-brown in color, narrow, elongated, and lacy, except the remiges and rectrices. The change in pigmentation usually extended over a larger area of the vane than did the loss of barbules. These modifications in plumage were, in general, proportional to the amount of thyroid tissue present at biopsy or post-mortem.

3. HORMONE THERAPY

a) Thyroid hormone.—Increased barbulation and black melanin formation have been reported following the feeding of desiccated thyroid (Greenwood and Blyth, 1929), as well as the injection of thyroxin (Emmens and Parkes, 1940) to thyroidectomized fowl. However, no data are available concerning the response of graded doses of thyroxin or the minimal dose necessary for the production of a normal feather. The effects of a single

dose of thyroxin and multiple doses at 6-day intervals have been studied.

The first visible effect of the administration of a single injection of 0.1 mg. thyroxin in a completely thyroidectomized rooster on the twenty-fourth or thirty-second day after plucking⁹ was an increase in barbulation, followed by a black melanin deposition in the web of breast, back, and saddle feathers (Fig. 13). The increased barbulation and melanin deposition formed a band across the growing feather which varied in length and width in different areas. The effect of this and higher doses was readily discernible within 24-48 hours after injection by a study of split feather-germ preparations.¹⁰ The melanin deposition continued for 4-6 days and formation of barbules for 8-10 days subsequent to the injection. A widening or broadening of the vane occurred in the feather area affected by the injection. The effect of such an injection was more conspicuous in the anterior than in the posterior breast feathers, as revealed by the length and width of the black webbed area. In the saddle a conspicuous, long, spindle-shaped area was formed by the increased barbulation and dark-red or black pigment. Proceeding posteriorly from its apex, the spindle shows a rapid widening, followed by a gradual basal taper. The longer duration of the effect of this dose in the saddle than in the breast was shown by the greater length of the webbed area.

The administration of a larger dose, such as two injections of 0.1 mg. thyroxin, each at 6-day intervals starting on

the twenty-second or thirtieth day after plucking,¹¹ resulted in increased barbulation and melanin deposition for a longer period and in a larger modified area than in cases receiving but a single injection. In the feathers observed, there was no complete reversion to the typical atrophic condition between the two injections. This was shown by the formation of a continuous band of black pigment and increased barbulation between the areas of maximum modification, which develop with each injection. This indicates at least a partial persistence of the effect of one such dose for at least 6 days. The area of barbulation and black pigment formed in the feathers after administration of the second dose was wider than the maximum of the first injection. This reaction, especially the increase in barbulation, was most conspicuous in the saddle. This dose and subsequent higher ones appeared to have a cumulative effect, since there was an increasing degree of modification with repeated doses, as revealed by the increased black melanin and barbulation of the saddle feathers.

With the administration of four injections of 0.1 mg. thyroxin each at 6-day intervals starting on the twenty-second day, the part of the feather developed after the second or third injection was typical of a normal rooster as concerns shape, barbulation, and color across the entire width of the vane (Fig. 14). While the tips of the breast feathers were reddish-brown, narrow, and lacy, their bases were solid black, broad, and webbed. The back feathers became broader and showed an excess of black, as compared to the normal rooster. The

⁹ Since growing feathers are known to record hormone modifications, feathers were plucked before their administration. In this way, regenerating feathers capable of modification by the hormone were available.

¹⁰ The sheath of a plucked feather papilla is split, which allows the unemerged feather to be spread flat on a slide for observation.

¹¹ The period of injection is given as the number of days which the feathers under observation have been regenerating. See Table 4 for details of the period of injection.

saddle exhibited a wider webbed area and a darker reddish-brown to black pigment than is normally present here.

While feathers displaying typically normal male characteristics on the entire vane (back and saddle) or a part of the vane (posterior and anterior breast) had been obtained, entirely normal feathers in all areas had not been produced with any of the previous doses. With the administration of fifteen injections of 0.05 mg. thyroxin each on alternate days from days 2-30, typically normal feathers were produced in the anterior and posterior breast areas (see Fig. 15). The breast feathers had broad round tips, were broad and fully webbed and solid black in color. The absence of reddish-brown pigment at the tips indicated that the entire feather developed under the influence of an effective dose of thyroxin. The back and saddle revealed barbulation and melanin deposition far in excess of normal. The tips of the back feathers had solid webs and showed more black melanin than normal. The web of the saddle extended the entire width of the feather and showed a broad area of black melanin.

A larger dose of thyroxin was required to produce normal color and form in the faster-growing feather areas, such as the posterior and anterior breast, than in the slower-growing areas, such as the back and saddle.

b) *Estrogenic hormone*.—The feminizing action of estrogens on the plumage of the Brown Leghorn is well known through the studies of Lillie (1942) and his associates and others. However, very little was known about the action of this hormone on the singularly modified plumage of thyroidectomized fowl. We were, therefore, interested in studying the possible role of the thyroid in the feminizing action of estrogens by observing their

effects on the athyroidic plumage of thyroidectomized roosters.

In the normal rooster and capon, daily administration of 23-36 γ ¹² of alpha-estradiol benzoate¹³ for two successive days, starting on day 14, was followed by the development of female plumage characteristics in growing feathers. A diamond-shaped, salmon-colored area, 5-8 mm. in length, was formed across the width of the vane on the anterior breast feathers. The back and saddle feathers developed a wider webbed area with a brown mottled pigment (Fig. 16). These modifications were similar to those observed by Lillie and Juhn (1932) following the administration of 7-8 r.u. of estrogen per 100 gm. of body weight.

The dose of estrogen necessary to produce henry plumage is proportional to the feather growth rate, so that the more rapidly growing feathers require a greater concentration because of their higher threshold than do more slowly growing feathers. Consequently, one might expect a lower dose in general to be required for feminizing of plumage in thyroidectomized roosters because of their lower feather growth rates (see Table 2). To determine the minimal amount of estrogen necessary to modify plumage pattern in thyroidectomized roosters, two successive daily injections of between 10 and 41 γ of estradiol were made in three adults. No significant modifications in the color or form of the feathers were exhibited by any of these individuals, even though the doses administered in each in terms of body weight were relatively much higher than required for feminization of plumage in the rooster or capon.

The daily administration of 30 γ of es-

¹² See Table 5 for dose per 100 gm. of body weight, on which all dosages are based.

¹³ Referred to hereafter as "estradiol."

tradiol for 15 days²⁴ was accompanied by only a slight modification in the breast but more extensive modifications in the back and saddle feathers (see Fig. 17). The anterior and posterior breast feathers exhibited a slight broadening of the web due to increased barbulation but no conspicuous increase in width of the vane, which remained hackled. The back feathers revealed an extension of barbulation but remained hackled. The vane became broader as a result of the assumption of a more obtuse angle between the barbs and rhachis and the lengthening of the barbs. The web showed a small amount of brown and black mottling. The saddle showed a slight broadening of the vane and a distinct increase in the width of the web. The web revealed a deposition of black melanin in varying amounts to form a distinct dark mottled pattern. These modifications became evident by the examination of split feather-germ preparations, 3-5 days after injections had begun. The greater response of the saddle to this and higher doses is probably the result of a lower threshold, as observed by Juhn, Faulkner, and Gustavson (1931) and Lillie and Juhn (1932) in the capon.

With the administration of higher daily doses of estradiol, such as 60 γ for 7 days, modifications of a similar character were observed. The saddle exhibited a marked increase in barbulation and black melanin, which showed some mottling. However, these feathers remained narrow and hackled. The back feathers showed similar modifications, though to a lesser degree. The breast also showed a slight increase in barbulation but no black melanin or mottling.

A marked modification of the breast feathers resulted from the daily administration of 109 γ of estradiol for 20 days

(see Fig. 18). Their apical ends revealed not only additional barbulation and broadening of the vane but also black melanin in a mottled pattern on a reddish-brown background. The amount of black melanin deposited was variable, though its presence was consistent. The back feathers showed extensive broadening, increased barbulation, and black and brown melanin in a mottled pattern. The saddle exhibited a widening of the web along the rhachis but remained narrow and retained a hackled margin. The web showed a more extensive deposit of black melanin, in a somewhat mottled pattern, than did the other feather areas. This pigmentation was much darker than that of the normal female.

With a larger daily dose of estradiol, such as 194 γ for 22 days, these modifications were not markedly enhanced in the breast feathers (see Fig. 19). In back feathers, and especially the saddle, hackling was generally lost, though the vane was not extensively broadened. This was the largest dose of estrogen administered, and it produced the greatest degree of barbulation and black and brown melanin formation.

For comparison with the complete operates, a Group I incompletely thyroidectomized rooster was treated daily for 8 days with 75 γ of estradiol, followed by 125 γ daily for 10 days. A greater degree of feather modification was produced than with the larger dose administered above in an athyroidic rooster (Fig. 20). The breast feathers revealed a larger amount of black melanin in a mottled pattern and a greater extension of barbulation than was found in any of the athyroidic roosters. The back feathers showed an extensive broadening of the vane, an increased barbulation, and a mottling of black and brown melanin. The saddle exhibited a widening of the web and vane but retained a narrow hackled region.

²⁴ See Table 5 for details of period of injection.

Its web showed a more extensive region of mottled black melanin than did the other feather areas. None of these feathers assumed the typical female pattern, though they had a more mottled pigmentation and a wider web than in the estradiol-treated athyroidic individuals.

Even with the large doses of estradiol used in completely and incompletely thyroidectomized roosters as compared with normal rooster and capon, a semblance of the typical female plumage was produced only in back and saddle feathers. These, however, did not exhibit the extensive broadening of the vane or the typical mottling of the pigment characteristic of the normal hen. With the doses used, the breast displayed an increase in barbulation, a broadening of the vane, and a deposition in the web of a dark-brown or black mottled pigment. The largest dose administered, even though much greater than that required to produce a typical female plumage in the normal rooster or capon, did not produce a plumage that was entirely henny in the athyroidic or nearly athyroidic rooster.

G. FEATHER GROWTH RATES

The feather growth rates of normal fowl have been shown to be modified by the administration of thyroid preparations (Torrey and Horning, 1925a; Domm, 1929b; Juhn and Barnes, 1931), as well as by estrogens (Domm, 1927; Domm and Gustavson, 1929; Juhn, Faulkner, and Gustavson, 1931) and by androgens (Juhn, Faulkner, and Gustavson, 1931). Therefore, we were interested in determining to what extent thyroidectomy influences feather growth rates in Brown Leghorn roosters and to see if the administration of thyroxin and estrogen in such individuals had the same effect on growth rates as follows their administration in normal individuals.

I. IN NORMAL FOWL

Since the characteristics of feather growth rates in Brown Leghorn roosters and capons are well known from previous investigations (Juhn, Faulkner, and Gustavson, 1931; Wang, 1945), a detailed analysis will not be presented. However, data are presented in Table 2 for comparison with that of athyroidic fowl.

The feather growth-rate increase at 10-12 days after plucking represents the transition in feather growth from Stage 1 (barb formation) to Stage 2 (beginning of shaft growth) (Lillie and Juhn, 1932). The average 2-day growth increment during the period of most rapid growth (days 24-36) was greatest in the posterior breast and least in the saddle. The difference in length relations of the feathers at the forty-eighth day compared with their length at maturity results from the sharp decrease in growth rate which occurs in all areas except the saddle after the forty-eighth day (see Table 2). Anterior breast and back feathers terminated their growth at 60-68 days and the posterior breast and saddle at 80 days after plucking. The feather lengths in the capon were greater than in the rooster, especially the posterior breast and saddle. Feather growth-rate averages for normal birds in the present study are based on feathers regenerated after each of four to six successive pluckings in a 1-year period.

No data were available on feather growth rates in bilateral poulards, shown by Domm (1927, 1929a) to develop the typical cocky plumage. In two bilateral poulards¹⁵ (YW, 134) on which growth rates were observed, the feather lengths and growth rates were of the same order as those of the rooster and capon (Table 2). The absolute feather length and

¹⁵ The bilateral poulards were obtained from a flock of such birds prepared and maintained by Dr. L. V. Domm.

growth rates were nearly identical with those of the capon.

2. IN THYROIDECTOMIZED ROOSTERS

Although a general retardation in feather regeneration has been noted in spontaneous (Landauer, 1929) and experimental (Parhon, 1924; Greenwood and Blyth, 1929) hypothyroid fowl, no observations were previously made on feather growth rates in the various body areas. Measurements of regenerating tail feathers in thyroidectomized Barred Plymouth Rock hen and rooster indicated a reduction in growth (Schwarz, 1930).

In the athyroidic rooster, the first stage (see p. 87) of feather regeneration was extended to 16–20 days after plucking, as compared to 9 or 10 days in the normal male. This estimate was based on the fact that an increase in growth rate occurred at this time in both types, which is characteristic for the transition point in feather growth between Stages 1 and 2. Regenerating feathers of the thyroidectomized male usually did not become measurable until 12–14 days after plucking, compared to 9 or 10 days in the normal. Feather regeneration was retarded to a lesser degree in the saddle, especially in the first stage, than in any of the other areas. This was readily demonstrable by the greater length of the saddle feathers, especially in the first 16 or 20 days of regeneration, when compared with the other feathers.

In four adult thyroidectomized roosters (Nos. 1355, 1362, 1392, and 3140) under observation, regenerating feathers continued growth with only a slight decrease as late as 80 days after plucking. This decrease appeared, first, in the anterior breast, which also terminates growth earliest in the normal male. At 80 days after plucking, the average lengths of regenerating feathers were similar to those

of feathers in comparable areas of the normal rooster at approximately 34 days for anterior breast, 36–38 days for posterior breast and back, and 46 days for the saddle (see Table 2). The average 2-day growth increment during the period of most rapid growth (days 24–36) was reduced but greatest for posterior breast feathers, followed in decreasing order by the saddle, the anterior breast, and the back. These differences in growth rates were reflected in their respective lengths at 48 days after plucking, when the posterior breast was longest and the anterior breast was shortest, thus differing from the normals. Though the growth rate of the posterior breast later exceeded the more rapid growth of the saddle feathers in Stage 1 of regeneration, the other feather areas continued to be slower growing than the saddle. The normally slow-growing feathers, especially the saddle, were less affected by thyroidectomy, so that the saddle was of greater length than the back, which, in turn, was of greater length and faster growing for a longer period than the anterior breast. Though the posterior breast undergoes a much greater reduction in growth rate than the saddle, its growth rate still exceeded that of the saddle, especially when the feathers were over 48 days old.

A comparison of the mean feather lengths in two normal roosters, two capons, and two bilateral poulards with four thyroidectomized roosters at 48 days after plucking gives a *P* value in all cases of < 0.0004 , which indicates a high statistically significant difference (see Table 3).

The average feather lengths and growth rates of three incompletely (Group I) thyroidectomized adult roosters (Nos. 940, 1231, and 3440) were greater than those of the complete operates. The order of growth-rate relations and ultimate feather lengths were similar to

those of athyroidic roosters (see Table 2). The accelerated feather growth rate of partially thyroidectomized roosters, though discernible in both the first and the second stages of feather growth, became more conspicuous with increasing age, especially in the second stage. The

breast. The saddle had a demonstrably longer period of rapid growth than the other areas, as shown by its greater length at 80 days, as in the normal. The normally faster-growing feather areas had a greater percentage decrease in growth rate than the slower ones. The

TABLE 3*
FEATHER LENGTHS AT 48 DAYS OF AGE FOR THE FIRST PLUCKING
(In Mm.)

BIRD	TYPE	FEATHER AREAS							
		Posterior Breast		Anterior Breast		Back		Saddle	
		L.	S.E.	L.	S.E.	L.	S.E.	L.	S.E.
1341.....	N	82.5±2.15		74.0±0.73		77.2±0.72		63.6±1.01	
1820.....	N	82.4±1.40		74.5±0.68		74.9±0.89		62.6±0.45	
1015.....	C	94.6±1.04		85.2±0.20		76.6±0.69		72.5±1.05	
1021.....	C	87.8±1.34		79.5±0.62		77.8±0.67		75.0±1.46	
YW.....	B	85.2±1.22		74.7±1.11		76.2±0.51		76.6±0.94	
134.....	B	87.9±1.42		74.1±1.21		73.8±1.53		80.9±1.54	
Mean.....		86.7		77.0		76.1		71.8	
1362.....	T	33.9±0.94		27.4±0.51		30.0±0.68		32.3±0.61	
1392.....	T	30.1±0.47		25.7±0.71		24.6±0.51		25.7±0.86	
3140.....	T	35.7±0.87		26.6±0.41		26.1±0.71		33.4±1.17	
1355.....	T	37.7±0.69		32.5±0.51		33.3±0.46		35.9±0.93	
Mean.....		34.3		28.0		28.5		31.8	
		$t = 38.6$ $P = < 0.0004$		$t = 38.4$ $P = < 0.0004$		$t = 55.6$ $P = < 0.0004$		$t = 20.2$ $P = < 0.0004$	

* Following is the list of abbreviations:
N = Normal rooster
C = Capon
B = Bilateral poulard
T = Thyroidectomized rooster

L. = Mean length
S.E. = Standard error of mean

first stage of feather growth extended to 18-22 days of age. The saddle length exceeded that of the posterior breast until 28-32 days, and equaled or was slightly less until 44-48 days. At 48 days the average length of posterior breast was greatest, followed in a decreasing order by the saddle, anterior breast, and back. In the period of rapid growth, 24-36 days after plucking, the average 2-day increment was most rapid for posterior

thyroid section available did not appear adequate for a differential stimulation of feather growth rates to their tract-specific limits.

3. HORMONE THERAPY

a) *Thyroid hormone*.—The administration of desiccated thyroid (Torrey and Horning, 1925a; Domm, 1929b; Jaap, 1934) or thyroxin (Larionov, 1931; Lillie and Juhn, 1932; Hardesty, 1935) in nor-

mal fowl has been shown to accelerate feather growth. In view of the stimulating effect of thyroxin in normal fowl, experiments were performed to investigate whether a similar reaction would occur in athyroidic birds. Since there was a conspicuous decrease in feather growth rates following thyroidectomy, studies were made to determine the minimal doses necessary for acceleration to their normal levels. A series of single and multiple doses of thyroxin was administered to athyroidic individuals after the plucking of appropriate feather areas. With the concentrations used, black melanin deposition and barbulation were increased to varying degrees in all areas. No toxic effects, which are readily manifested by a blanching of feathers, were visible.

In the thyroidectomized rooster, the injection of 0.1 mg. of thyroxin was followed by a sharp increase in the growth rate of feathers for 10-12 days, returning to normal 4-8 days later (14-20 days after injection) (see Table 4). The stimulating effect of this and higher doses could be observed within 2 days after administration. The average 2-day growth increment for the period of 6 days following injection was most rapid in posterior breast feathers and least in back and saddle. While these growth rates were higher than those of the untreated thyroidectomized rooster, they were not so high as those of the normal rooster.

With the administration of two doses of 0.1 mg. thyroxin at a 6-day interval, the 2-day growth increment for the 6-day period following the second injection showed a further acceleration (see Table 4). A comparison of the growth rates attained when the same dose was administered at different feather ages revealed a higher rate when the injections were made on days 30 and 36 after plucking than earlier. This may be due to the

greater responsiveness of feathers known to prevail at this age.

Greater stimulation was obtained by four injections of 0.1 mg. thyroxin at 6-day intervals (see Table 4). During the period of 6 days following the second injection, the feather growth rates represented the maximum obtained for the posterior breast and the near maximum for the other regions. The growth rate of the posterior breast feathers was closer to normal than the other areas. During the 6 days after the fourth injection, the back and saddle continued to show an increase in growth rate, while the breast showed a decrease. The anterior breast had a sharper and more rapid decrease in growth rate following cessation of medication than did the posterior breast.

The continued small increase in growth rate of the back and saddle after the breast had reached its maximum with this dose and higher ones resulted from their longer period of normal growth and lower threshold, which allows a longer period of response. The feather growth acceleration following thyroxin administration persisted for 10-14 days after the last injection. This period is somewhat dependent upon the age of the feathers at the last injection, a factor known to influence their responsiveness.

The maximum growth rates attained following the administration of four injections of 0.15 mg. thyroxin, each at 6-day intervals, were equal to or slightly less than that obtained with four successive injections of 0.1 mg. thyroxin (Table 4). The attainment of a lesser growth rate in the anterior and posterior breast feathers here than with 0.1 mg. thyroxin injections probably resulted from the fact that these injections were begun at a sufficiently later feather age to encounter the period of decreased responsiveness known to prevail toward the end of

the growth period of a feather. The back and saddle, however, reached a higher growth rate here than with previous doses. This may result not only from a greater stimulation with a higher dose but also from the continued responsiveness of slower-growing feathers at the later stages of growth. The average growth increment of the saddle feathers after the third injection equaled or exceeded the normal rate.

Since normal feather growth rates were not obtained throughout with the thyroxin doses employed, fifteen alternate-day injections of 0.05 mg. thyroxin were administered (Table 4). This procedure provided a more constant and longer period of medication. The administration of this dose was followed by stimulation of feather growth rates to the normal or even greater levels.

The time of appearance of the feather

TABLE 4*
EFFECT OF THYROXIN ADMINISTRATION ON FEATHER GROWTH RATES
IN THYROIDECTOMIZED ROOSTERS

BIRD	DOSE (MG.)	INJ. DAYS A	FEATHER AREAS	2-DAY GROWTH RATE INCREMENTS					
				Days Measured					
				Pre-Injection	Post-Injection				
1392.....	0.1	{24 or 32	R-14-0	0-6	0-12	12-28			
			Post. br.	2.2	3.3	3.2	2.4		
			Ant. br.	2.1	2.7	3.0	1.8		
			Back	1.6	2.6	2.5	1.9		
			Saddle	1.6	2.6	2.5	1.8		
1392.....	0.1	{22, 28 or 30, 36	R-10-0	0-6	6-12	6-14	6-18		
			Post. br.	1.7	3.0	4.2	4.1	3.7	
			Ant. br.	1.9	2.6	3.5	3.3	2.3	
			Back	1.8	2.6	3.6	3.4	2.3	
			Saddle	2.2	2.6	2.7	2.8	2.0	
1362 [†]	0.1	{22, 28, 34, 40	R-10-0	0-6	6-12	12-18	18-24	28-38	
			A 12-22	22-28	28-34	34-40	40-46	50-60	
			Post. br.	1.3	3.1	4.4	4.1	2.2	
			Ant. br.	1.1	3.1	4.0	4.2	3.8	1.5
			Back	0.9	2.8	3.9	4.1	4.2	2.1
1362 [†]	0.15	{26, 32, 38, 44	R-10-0	0-6	6-12	12-18	18-24		
			A 16-26	26-32	32-38	38-44	44-50		
			Post. br.	1.5	3.3	4.3	4.0	3.9	
			Ant. br.	1.2	3.5	3.8	3.9	4.0	
			Back	1.1	2.9	3.7	3.7	4.1	
1392 [†]	0.05	{2-30, alt. days	R 10-14	14-24	14-34	36-46			
			A 12-16	16-26	16-36	38-48			
			Post. br.	3.4	5.4	5.0	2.3		
			Ant. br.	3.0	4.8	4.5	1.1		
			Back	2.7	5.0	4.5	1.6		
1392 [†]	0.05	{2-30, alt. days	Saddle	3.2	3.8	4.1	2.9		

* Following is list of abbreviations:

R = Days of measurement in relation to injection time

A = Actual days of injection based on feather age

† = Average of right and left feather areas

vane above the surface of the skin was similar to normal, though at comparable ages, such as 10-14 days, the respective feathers here were longer. The time of transition between the first and second stages of feather development (see p. 87) was still delayed when compared with the normal. It occurred 16-18 days after plucking, as indicated by the sharp rise in growth rate at this time. As with the lower doses, the normally faster-growing feathers were stimulated most and revealed the greatest growth rate. During the sixteenth to twenty-sixth days after injections had begun, the maximum 2-day feather growth increments were attained. The saddle continued to increase after this period, reaching its 2-day maximum growth rate, 4.1 mm., in the period between days 22 and 32. This thyroxin dose appeared capable of accelerating the initiation of the first and second stages of feather development and growth.

The feathers showed only a slight decrease in growth by the sixth day after cessation of medication with this concentration, after which a sharp decrease was noted. The period of sustained rapid growth after cessation of medication was less here than was observed in other cases. This was probably due to the greater length and maturity of the feathers and the consequent decreased reactivity. Saddle feathers exhibited a more gradual decrease in growth rate, which extended over a longer period than for the feathers of other areas. In this thyroxin-treated athyroidic rooster the accelerated regenerating plumage, except for the saddle, terminated its growth at an age closer to that of the normal rooster than in any of the other treated cases. This was probably related to the tract specificity for feather length.

b) *Estrogenic hormone*.—The feminizing action of estrogens on the pattern

and growth rate of developing feathers is well known through the work of Domm and Gustavson (1929), Juhn, Faulkner, and Gustavson (1931), and others. Juhn, Faulkner, and Gustavson (1931) observed that, following the administration of appropriate doses of estrogenic hormone, anterior and posterior breast feathers of the capon showed a decrease in growth rate, while the back and saddle showed an increase, thus approximating the growth rates observed in the hen. In view of the observed feather growth-stimulating effects of estrogens, it seemed desirable to determine whether the thyroid played any role in this growth-promoting action. The slow-growing feathers of the thyroidectomized roosters were judged to furnish ideal material for the solution of this question.

Following two or more injections of 34 γ of alpha-estradiol benzoate¹⁶ in the capon, feather growth rates became similar to those of the female in the respective feather areas as observed by Juhn, Faulkner, and Gustavson (1931) (see Table 5). The anterior and posterior breast feathers showed a decrease in growth rate, while the saddle revealed an increase. The rate of the back feathers was somewhat variable but generally lower.

Two successive daily injections of estradiol ranging from 10 to 39 γ of estradiol in three thyroidectomized roosters revealed no significant modifications in growth rate. The daily administration of 30 γ of estradiol for 15 days was followed in all areas by a 10-15 per cent increase in growth rates over untreated controls (see Table 5). The increase was greatest from the eighth to the sixteenth day after the start of medication. Conspicuous was the lesser increase in the growth rate of

¹⁶ See Table 5 for dose per 100 gm. of body weight, on which the total dose has been calculated.

saddle feathers as compared to the other areas. It required a 4-6-day period of medication before a modification with this and higher doses was revealed. The growth rate returned to the untreated level within 4-6 days after cessation of medication.

The daily administration of higher doses resulted in a further acceleration of

growth rates. With a dose of 49 γ for 20 days, the anterior and posterior breast showed an increase of 10-15 per cent, while the saddle revealed none (see Table 5 for the data of these experiments). The administration of 60 γ for 7 days resulted in a 25-30 per cent increase in feather growth rates. Further increases in growth rates to as much as 50 or 60

TABLE 5*

FEATHER GROWTH RATES FOLLOWING ADMINISTRATION OF ALPHA-ESTRADIOL BENZOATE

BIRD	TYPE	INJ. DAYS (A)	DOSE PER INJECTION		FEATHER AREA	2-DAY GROWTH-RATE INCREMENTS									
			$\gamma/100$ Gm.	Total γ		Experimental					Control				
1211 ¹	T	$\left\{ \begin{array}{l} 18-32 \\ \text{or} \\ 22-36 \end{array} \right\}$	2.3	30	Post. br. Ant. br. Back Saddle	R 0-8 2.1 1.5 1.8 1.1	8-16 2.8 2.9 2.7 2.3	16-26 2.5 2.8 2.7 2.2	24-34 2.4 2.5 2.4 2.0		A 18-26 2.4 1.4 1.9 1.8	26-34 2.5 2.3 2.2 2.2			
3140.....	T	26-40	3.5	49	Post. br. Ant. br. Saddle	R 0-8 A 20-26 2.7 2.7 2.8	8-16 26-34 2.9 2.7 2.5	16-26 30-40 3.0 2.9 2.6	24-34 34-42 2.7 2.7 2.3	42-52 52-60 2.4 2.6 2.1	26-34 34-44 2.4 2.6 2.6	28-34 34-44 2.5 2.6 2.7			
1362 ²	T	24-30	5.0	60	Post. br. Ant. br. Back Saddle	R 0-8 A 16-24 1.6 1.2 1.0 1.9	8-16 24-32 2.4 2.3 2.0 2.2	16-26 28-34 2.8 2.7 2.6 2.3	24-34 34-44 2.5 2.5 2.5 2.2		24-32 28-34 2.3 2.0 2.2 2.0	26-34 34-44 2.2 1.5 2.0 1.9			
1362 ²	T	$\left\{ \begin{array}{l} 0-19 \\ \text{or} \\ 4-23 \end{array} \right\}$	10.0	109	Post. br. Ant. br. Back Saddle	R 8-14 1.3 0.9 1.3 1.4	14-24 3.2 3.0 3.2 2.7	24-34 2.5 2.6 2.8 2.2	34-44 2.7 2.6 2.8 2.3		A 20-28 2.3 2.0 2.1 1.9				
1392.....	T	$\left\{ \begin{array}{l} 0-21 \\ \text{or} \\ 4-25 \end{array} \right\}$	16.5	194	Post. br. Ant. br. Back Saddle	R 14-24 1.9 1.8 1.9 1.9	24-34 2.8 2.6 3.0 2.7				A 14-24 1.2 1.3 0.8 1.3				
1015.....	C	14,15	1.3	34	Post. br. Ant. br. Back Saddle	R 0-4 A 12-14 4.3 3.4 2.3 3.0	4-6 14-18 3.9 2.8 2.0 3.8	6-10 18-20 6.3 5.3 4.4 3.2			12-14 4.3 3.4 2.2 3.1	14-18 4.8 3.8 2.5 3.2	18-20 6.3 5.3 4.4 3.9		

* Following is list of abbreviations:
R = Days of measurement in relation to time of injection
A = Actual days of injection and measurement in terms of feather age
1 = Right and left side feather areas measured
T = Thyroidectomized rooster
C = Capon.

per cent over controls were obtained with a dose of 109 γ of estradiol for 20 days. In the latter experiment the maximum 2-day growth rate was attained between the fourteenth and the twenty-fourth day after start of medication. In these experiments the greatest increase in feather growth rate was manifested by the breast and the least by the saddle.

The daily administration of 194 γ of estradiol for 22 days was also followed by an increase of 50-60 per cent in feather growth rates (see Table 5). The increased growth rate was discernible at 14-18 days of age, at which time the feathers first became measurable. A further sharp increase in growth rate was discernible after cessation of medication and persisted for 18-22 days thereafter. This may be a result of medication during the early development of the feathers (for 25 days, starting on day of plucking) when they are known to have a high degree of responsiveness. The saddle feathers were observed to maintain growth rates more similar to the posterior breast, which is different from the results with lower doses. The similarity of growth rate of the anterior breast feathers to that of the posterior breast and saddle was conspicuous. This would indicate a tendency for equalization of growth rates, as is typical of the hen or occurs after estrogen administration in the normal capon. While the feather growth rates showed an increase with the doses administered, the rates typical of the normal hen were not attained. The acceleration of feather growth may result from the characteristic stimulating effect of estrogens on feathers growing slower than the normal female rate.

IV. DISCUSSION

The modifications observed following thyroidectomy in this investigation were, in general, more drastic than those re-

ported by previous investigators. This is probably due to the more careful distinctions made between complete and incomplete thyroidectomy, as well as to the larger number of birds examined and the longer period of observation.

The retardation in body growth may result from a modification of pituitary function and basal metabolism, which is known to follow thyroidectomy and upon which growth is dependent. The pituitary cytology of thyroidectomized pigeons (Schooley, 1937) and chickens (Payne, 1944) is reported to be similar to that of dwarf chicks with undeveloped thyroids (Payne, 1944). An inhibition of the production and/or secretion of the pituitary growth-stimulating hormone has been reported following thyroidectomy in rats (Flower and Evans, 1924; Scow and Marx, 1945). Smith (1933) suggested that thyroxin stimulates growth in thyroidectomized rats by restoring normal pituitary function.

The metabolic level in birds has been shown to decrease following thyroidectomy (Marvin and Smith, 1943) and to be dependent upon the degree of thyroid activity (Riddle, 1932; Miller, 1938). In normal chicks, body growth can be stimulated by the oral administration of small doses of iodocasein (Irwin, Reineke, and Turner, 1943) or thyroxin (Simmons, 1943). Hammett (1926) suggested a growth-promoting action for the thyroid secretion by reason of its production of an increase in cell size in contrast to an increase in cell number by the growth hormone of the pituitary.

The thyroid appears to have a general calorogenic action, as well as a specific action on other endocrines. The simultaneous decrease in the thyroid hormone and the pituitary growth hormone leads to such a striking modification of body growth because of their synergistic action (Evans, Simpson, and Pencharz,

1939). Salmon (1936) postulated that the thyroid was responsible for development of the capacity to respond to other hormones. The larger size of incompletely thyroidectomized birds probably results from their higher level of pituitary growth hormone and its greater utilization as a result of the availability of some thyroid secretion.

Previous observation on thyroid-pituitary-gonad relations indicates both a direct and a secondary control of gametogenic activities by the thyroid. The administration of an adequate dose of desiccated thyroid (Crew, 1925; B. M. Zawadowsky, 1925*a*) or thyroxin (Aron and Benoit, 1934) to normal sexually quiescent birds or thyroidectomized birds (Winchester, 1939; Greenwood and Chu, 1939) leads to an augmentation of gonad activity.

The importance of the secretions of the anterior lobe of the pituitary in the development and maintenance of the activity of the gonads has been demonstrated by Domm (1937). A reduction in gonadotropic potency of the pituitary after thyroidectomy has been reported in mammals (Evans and Simpson, 1930; Van Dyke and Ch'en, 1933; and others). Smelser (1939) suggested that the decreased gonadal activity of thyroidectomized rats resulted from a decrease in the amount of gonadotropic hormone secreted into the blood. Benoit (1936, 1937) observed an increase in the gonad activity of thyroidectomized drakes after exposure to light. He considered this to result from the increase in pituitary gonadotropic activity known to follow such treatment (Benoit, 1935).

The decreased size of the seminiferous tubules and inhibition of gametogenesis following thyroidectomy would, therefore, seem to result from (1) an absence of thyroid secretion, which probably acts to stimulate tissue growth by its control of

metabolism; (2) a decrease in secretion or potency of pituitary gonadotropic and growth hormones, known to follow thyroidectomy; and (3) a decrease in ability to utilize the available pituitary hormones as an aftermath of the reduced basal metabolism. Incompletely thyroidectomized roosters show a greater amount of testis growth and gametogenic activity than complete operates, owing probably to the fact that the former have thyroid secretion available and, consequently, an increased production and utilization of pituitary hormones. The degree of development is related to the amount of thyroid present. This has also been noted by others (Greenwood and Chu, 1939). These investigators also suggest an intermediary role for the pituitary in the inhibition of gametogenesis observed after thyroidectomy.

Since comb growth is known to be dependent on androgens (McGee, Juhn, and Domm, 1928; and others), it is logical to assume that the decreased comb size of thyroidectomized roosters may be the result of an insufficient androgen secretion or utilization in such individuals. However, the absence of a capon-like condition in these characters in such individuals indicates that androgen production or its utilization is never completely suppressed.

In the presence of thyroid secretions there is probably a stimulation of pituitary gonadotropic hormone and androgen secretion (Smith, 1933), as well as an increase in ability to use these hormones (Salmon, 1936). This accounts for the increase in comb size observed in this investigation after injections of thyroxin and after feeding of desiccated thyroid to thyroidectomized fowl by Greenwood and Chu (1939) and to normals by Crew (1925). The interrelation of thyroid and testicular secretions in comb growth is also shown by its greater size in partially

thyroidectomized roosters of this and previous investigations (Schwarz, 1930; and others). The stimulating influence of thyroid secretions was shown by the greater comb growth of capons (Simmons, 1943) and in capons as well as thyroidectomized roosters in my experiments after the simultaneous administration of thyroxin and testosterone than following either alone.

The reduced spur development following thyroidectomy cannot be considered to result from an absence of gonadal hormones, since estrogens inhibit initiation of spur growth, while androgens exercise a retarding effect on their development (Domm, 1927). The decreased spur growth in thyroidectomized roosters was probably a result of the combined effects of a reduced tissue metabolism and a deficiency of pituitary growth hormone which led to a reduction of general body growth (see above).

The slowing of nervous reactions and dulness of the sensorium occurring concurrently with the decrease in basal metabolism characteristic of hypothyroidic individuals (Thompson, 1942) probably led to the lethargy of thyroidectomized roosters. The lethargy of cretinism is treated by increasing the basal metabolism with thyroxin medication (*ibid.*). The absence of mating behavior and crowing in the athyroidic roosters may result in part from the general apathy of hypothyroidic individuals and possibly from an inadequate utilization of androgen.

Except for one short-lived case of a possible complete thyroidectomy reported by Greenwood and Blyth (1929), all previous observations on feather modifications in Brown Leghorn roosters and capons were probably based on incomplete operations. This is indicated by the lesser degree of pigment and barbulation modifications than that observed in the

athyroidic males of my experiments and and by the ultimate reversion to normal plumage after the molt in many of the cases (Greenwood and Blyth, 1929; Parkes and Selye, 1937; Emmens and Parkes, 1940). The absence of black or slate pigment in the fluff portion of the feather was not previously noted. Most of the plumage modifications in preceding experiments were similar to that of Group I or Group II incompletely thyroidectomized roosters discussed in this paper (see pp. 82-83). Extensive debarbulation has been observed in some cases of toxic hyperthyroidism which was believed to result from an abnormal metabolism (B. M. Zawadowsky, 1925a, b; Cole and Hutt, 1928).

The differences in hormone threshold among the various feather areas or within individual feathers (Lillie and Juhn, 1932) are reflected in the degree of feather modification observed after thyroidectomy. The uniform and complete loss of normal pigments and barbulation in a particular feather or feather area indicates that the level of thyroid secretion was below that necessary for their production. The persistence of a slate-colored pigment in the fluff portion of some feathers or black melanin in parts of the primary and secondary flights and tail feathers in completely thyroidectomized roosters may indicate that the thyroid secretion is not necessary for its production in the feathers of these areas. Since the main tail feathers have a higher threshold for estrogens than other body areas (Domm, 1927) and inasmuch as the thresholds for thyroid generally conform to those for estrogens, one would expect a loss of black pigment in these feathers as in those of lower thresholds. At present no suitable explanation is available for the persistence of black pigment in the tail and flight feathers. Greenwood and Blyth (1929) and Emmens and

Parkes (1930) agree that the regionalization of feathers and differences in pigmentation and form within the individual feather are the result of their threshold differences.

The observed difference in hormone threshold in the bilateral halves of an individual feather has made possible the experimental production of a modification in only one half-vane of a feather (Lillie and Juhn, 1932). The presence of a dark, reddish-brown pigment on the outer vane of the normal secondary flight feathers would indicate that a higher level of thyroid secretion was necessary here for the production of black melanin than on the inner vane. The unilateral difference in the degree of modification obtained in these feathers after thyroidectomy (a greater loss of black melanin on the outer half-vane than on the inner one, which was replaced by reddish-brown pigment) seems to conform to this difference in threshold.

In partial thyroidectomies the hypothyroid modifications were frequently manifested as a "tipping" or "bar-ring" of feathers in a manner similar to that noted by Domm (1927) in ovariectomized fowl. In all feather areas of incomplete operation there was a more extensive loss of black melanin than of barbulation, which indicates that a higher threshold of thyroid secretion was necessary for black melanin production than for maintenance of barbulation. This conclusion conforms with the data obtained from thyroid feeding (Domm, 1929b) or thyroxin injection (Juhn and Barnes, 1931; Lillie and Juhn, 1932).

The diversity in degree of alteration of the feather areas in partially thyroidectomized roosters resulted from an oscillation in the amount of thyroid secretion available owing to thyroid regeneration or removal and the differential in feather thresholds. Since faster-growing feathers

have a higher threshold than the slower ones (Juhn, Faulkner, and Gustavson, 1931; Lillie and Juhn, 1932), more extensive and conspicuous plumage modifications occurred in the faster-growing posterior and anterior breast than in the slower-growing back and saddle feathers.

A variation in degree of modification was also observed within individual feathers of incomplete thyroidectomies by others (Greenwood and Blyth, 1929; Emmens and Parkes, 1940). These result from differences in the reaction thresholds within the individual feather (Lillie and Juhn, 1932) and variations in the level of thyroid secretion. Even when the level of thyroid secretion is kept constant for the period of a feather's axial growth, an unequal degree of modification occurred, probably as a result of threshold differences over the length of the feather. The development of a black melanic area at the apex of some feathers, otherwise hypothyroid, may be associated with the slow growth rate in the first stage of feather development (see p. 87), when these barbs are formed, while the development of black melanin at the base of these feathers is, no doubt, associated with the slower growth rate and the concurrently decreased threshold occurring at the approach of feather maturity. The decrease in threshold from apex to base of the barbs (Lillie and Juhn, 1932) results in the appearance of signs of thyroid deficiency at the apex of the barbs (margin of vane) sooner and to a greater degree than at their bases (rhachis area).

The area of increased barbulation following thyroxin administration usually exceeded black-pigment formation, which was in accordance with the higher threshold required for the production of the latter. The melanin and barbulation formed in the saddle were in excess of those normally present here, which indi-

cates that 0.1 mg. of thyroxin was above the minimal dose necessary to bring about development of the normal condition in this area. The spindle-shaped black melanic area formed about the rhachis after thyroxin administration illustrates the relation of thyroid level and feather threshold to the extent of modification. Proceeding posteriorly from its apex, the spindle shows a rapid widening, which indicates a rise in thyroxin concentration. The widest part of such a spindle is above its center, indicating a more rapid absorption than excretion. The basal taper of the spindle indicates a gradual lowering of the thyroid level. This reaction is in accord with the known rise in threshold of reaction from the base to the apex of the barbs (Lillie and Juhn, 1932).

The development of a cocky plumage in the capon and bilateral poulard indicates its independence of gonadal secretions (Domm, 1927, 1929a). The dependence of cocky plumage on a certain level of thyroid secretion for its maintenance has been suggested by Greenwood and Blyth (1929). This is supported by the re-appearance of the normal plumage pattern in my thyroidectomized roosters following thyroxin administration.

The development of "female-like" characters, such as a sparse mottling and an extension of barbulation in the athyroidic feathers of the rooster following estradiol administration, rather than the dense mottling and solid-webbed vane such as develops in the normal rooster following such medication, reopens the question of the role of thyroid and ovarian secretions in development of the female plumage pattern in Brown Leghorn fowl. Do thyroid and ovarian secretions have a parallel, complementary, or synergistic effect in the development of female plumage?

Greenwood and Blyth (1929) believed

that "the former (ovary) stimulates the latter (thyroid) to a higher level of activity than that present in the male, and so indirectly causes a hyperthyroid effect on feathers," as seen by the extensive barbulation in the hen plumage. "At the same time, it (ovarian secretion) modifies this condition by acting directly on the feathers and restricting deposition of melanin." The author is inclined to agree with Fraps and Burrows (1939) that this does not appear to be a valid conclusion, since the basal metabolism of the rooster (Mitchell and Card, 1927), as well as the male pigeon (Riddle, 1932), is generally higher than that of the female.

Fraps and Burrows (1939) suggested a complementary action between ovarian and thyroid secretions in the production of female plumage pattern. This was based on their obtaining an extension of black melanin followed by a blanching of the feather in a thyroidectomized capon after injection of large doses of theelin. The blanching effect is regarded as a typical toxic reaction in normal fowl. The modifications in the saddle feathers were less marked than in the posterior breast, which would not be expected on the basis of their thresholds.

In thyroidectomized roosters, thyroxin brings about the development of an area of solid black melanin and barbulation, whereas estradiol not only stimulates an extension of barbulation but also a mottling of black or brown melanin. When both thyroid secretions and estrogens are available, as in the hen, a female pattern is produced. The inability to produce this pattern in an estradiol-treated athyroidic rooster may indicate that the function of the thyroid is to increase the ability of the feather germ to utilize the estradiol. This conclusion is supported by a report of the development of the female pattern in an incompletely thyroidectomized capon following theelin administration

(Fraps and Burrows, 1939). Similarly, in my experiments a greater amount of barbulation and mottling of black and brown pigment was produced in an incompletely thyroidectomized rooster (No. 3440, p. 86), which had received only a small dose of estradiol, compared to that of complete operates.

My results on injection of alpha-estradiol benzoate in athyroidic roosters indicate a synergistic action between estradiol and thyroxin in development of the female pattern. The greatest degree of modification was observed in the slow-growing feather areas, which conforms to their lower threshold. The failure to develop a typical female pattern after estradiol administration may be due to (1) an inability of the feather germ to utilize adequately the hormone in the absence of thyroid secretions or (2) the fact that the estradiol may be excreted too rapidly to permit its utilization. In normal fowl the administered estrogens are utilized at a sufficiently rapid rate to be effective before they are excreted.

To account for the replacement of the normal pigments by a reddish-brown pigment after thyroidectomy, it is necessary to consider whether these pigments are the product of the same or of different melanophores. Though the plumage melanoblasts originate in the neural crest (Danforth, 1937; Dorris, 1939), they may undergo various modifications after migration to the dermis (Waterson, 1942; Foulks, 1943). Wang (1943) favors the "monophyletic theory" of pigment formation, in which only one type of melanophore is involved in the production of both black and red pigment, possibly under the differential control of the epidermal substratum. This would imply that the melanophores are dependent in some specific manner upon the feather-forming epidermis. Willier (1942) favors the view that both the red and the black

types of melanophores are present. Whether black or red pigment is to be formed lies under control of the follicular epidermis. Hamilton (1940), from *in vitro* studies, found no evidence for the conversion of one kind of melanoblast into another. In order to yield red melanoblasts, a bird would need to have a genetic constitution for the synthesis of red pigment. Hamilton (1941) found two distinct cell types, but no intermediate types.

Ladebeck (1921) reported the existence of transitional forms from black to red in the granules of Brown Leghorn feathers. This would suggest that red-brown and black were successive stages in the process of pigment formation by a single type of melanoblast. Bohren, Conrad, and Warren (1943), however, could not conclusively find such a differentiation of granules either by morphological or by chemical criteria.

In normal (Lillie and Juhn, 1932) and thyroidectomized Brown Leghorns, melanophores producing one kind of pigment may be completely replaced by those producing another within less than 24 hours after the injection of hormone. Both before and after such a change the barb ridges may be densely packed with pigment cells. The promptness and completeness of the color changes elicited by hormones (as pointed out by Danforth, 1937) make it seem improbable that the hormones are merely acting selectively upon two types of melanophores previously determined with respect to type. Willier and Rawles (1944) have considered that the melanophore precursors are fixed as either black or red after entering the epidermis of the developing feather. Their reference to "precursor melanophore" may indicate that they believe it to occur at some time before the beginning of pigment formation. Wang (1943) has shown that the feather

papilla epidermis is the controlling factor for melanophore determination and that this is probably determined concurrently with other morphological criteria of tract specificity.

Since pigment alterations appeared concurrently with modifications in growth rate, a difference in metabolic rate may be involved. The influence of thyroid secretion on basal metabolism has been shown in the pigeon (Riddle, 1932; Marvin and Smith, 1943) and the sparrow (Miller, 1938). Lillie and Wang (1941) have suggested that the development of certain composite colors from a combination of breast and saddle half-papillae, which results from a replacement of saddle cells by those of the breast, might be associated with some intrinsic property related to the breast's higher growth rate. Faulkner (1932) proposed the theory that black pigment was formed in feathers whose growth rate exceeded a certain level, and that, below this rate, red pigment was formed. However, no explanation was offered for feathers whose pigment does not correspond to her growth-rate scale or those which have both black and red pigments.

A correlation between basal metabolism and plumage pattern is suggested by the close association of feather structure and pigment with growth rate. The rapidly growing feathers of the male breast have a black pigment on a wide and well-developed web. The slower-growing feathers, such as back and saddle, exhibit black and red pigment on a hackled vane. The saddle, which has the slowest growth rate, shows the greatest amount of red pigment and hackling. The administration of thyroxine in the rooster or capon (Lillie and Juhn, 1932) was followed by an increase of black pigment and barbulation in the back and saddle, concomitant with an increased growth rate. The administration of estrogen in

the rooster stimulated an increase in feather growth rate, formation of black and brown pigment, and barbulation in back and saddle feathers (*ibid.*).

In the red-pigmented feather areas of normal and thyroidectomized fowl, a certain physiological substance or process necessary for oxidation of tyrosine or dopa into black melanin may be lacking in the follicles. Dorris (1939) suggested the existence of an "inhibitor" to the synthesis of black melanin. The production of such a substance by the male saddle epidermis may account for the absence of black here (Wang, 1943). Another possibility is that the chain reaction affecting the oxidation of dopa into black melanin ceases at an intermediate stage, at which the oxidation product is a red-brown pigment. This would be confirmed by establishment of the existence of intermediate granule stages between black and red, as reported by Ladebeck (1921). The latter may be the result of a mere quantitative difference, as, for instance, in the oxygen content of the oxidases (Wang, 1943).

The existence of a single stem cell which has the capacity to differentiate into either a black or a red melanophore is supported from a chemical point of view. A red-colored substance has been shown to be an intermediate product in the oxidative action of tyrosinase on tyrosine to black melanin. (Raper, 1932). However, Nickerson (1946) has obtained an *in vitro* oxidation of black melanin or dopamelanin to a product whose solubility and absorption spectrum are similar in some respects to those of natural red melanin. Figge (1940) has found the production of melanin from tyrosine by tyrosinase to be regulated by the oxidation-reduction potential of the substance added to the reaction mixture. A red pigment is formed at a lower redox potential than is black. He (*ibid.*) states

that "the normal pigmentary . . . alterations associated with physiological changes or sex hormones . . . are but visual evidence of a change in the oxidation-reduction potential of melanogenic centers in the cell."

The marked reduction of black pigment in thyroidectomized fowl may result from a decreased oxidation-reduction potential, a direct hindrance of the dopa or tyrosine oxidation in the absence of thyroid secretion, or the decreased metabolism and growth rates of the feather follicle. Faulkner's (1932) hypothesis would indicate that the absence of black pigment in athyroidic fowl is a result of the decreased feather growth rates. The simultaneous inhibition of black melanin production and feather growth rates after administration of thiouracil to normal fowl (Domm and Blivaiss, 1944, 1946) conforms to the proposed relation of plumage pigment production to basal metabolism and feather growth rates.

No conclusive data are available as to the existence of one or two types of melanophores. It appears feasible to assume that, in the absence of thyroid secretions, either (1) the pro-pigment in the melanophores can be oxidized only to the red-brown stage or (2) only those melanophores which have red-brown as their end-product are able to undergo oxidation. These reactions probably occur under the control of the epidermis.

The reduced feather growth rates of athyroidic individuals need to be considered on the basis of their reduced metabolic level and pituitary growth hormone secretion. Gonadectomy does not result in such a retardation as seen from the feather growth rates of capons and poulards. However, feather growth acceleration has been shown to follow thyroid or thyroxin administration in normal fowl (Torrey and Horning, 1925a; Domm, 1929b; Lillie and Juhn,

1932). Lillie and Wang (1940) have suggested a correlation between basal metabolic rate and the growth rate of feathers. The close relation between thyroid activity and feather growth was indicated by the development of feathers in chicks in correlation with an increase of thyroid activity as determined by secretory action and iodine content (Chaudhuri, 1928; Benozzi, 1932).

The more rapid growth rate of the posterior breast than of other feather areas in thyroidectomized roosters suggests the existence of a basic order of feather growth rates.¹⁷ The fact that a similar relation occurs in normals suggests that their higher metabolism results in an acceleration of feather growth rates which is roughly proportional to the basic order observed in athyroidic males. The tendency toward an equalization of feather growth rates in thyroidectomized roosters is conspicuous. The existing differences may represent a response to a nonthyroid metabolic stimulant or the prevailing metabolic level. The more rapid growth rate of the saddle compared to anterior breast and back feathers may represent the response of a low threshold feather area to a small but constant level of stimulation.

The need for a larger dose of thyroxin to stimulate and maintain an increase in feather growth rates in the posterior breast than in the saddle emphasizes threshold differences. The apparent existence of a tract specificity for the rapidity of growth to which the feathers could be stimulated was shown by the saddle feathers. For instance, with doses of thyroxin in excess of the amount necessary for acceleration to its normal growth rate, the saddle would not exceed its normal rate or approximate the higher rate

¹⁷ A similar order of feather growth-rate relations has been found in thyroidectomized hens (Blivaiss and Domm, 1944).

of the posterior breast. This may be due to an inability of the epidermal follicular cells of the saddle to exceed a certain metabolic level which would influence the growth rate.

Further clarification of the relations between plumage pattern and growth rates and gonad and thyroid secretions may be obtained from a study of effects of the simultaneous administration of thyroxin and estrogens or androgens in thyroidectomized capons and bilateral poulards. It is conceivable that the relation of basal metabolism to plumage pattern and growth rate can be observed by a study of the effects of a nonthyroid metabolic stimulant. A careful study of the alterations in pituitary and adrenal gland histology and in secretions after thyroidectomy might facilitate interpretation of some of the problems discussed in this paper.

V. SUMMARY AND CONCLUSIONS

1. A study was made of the relations between body growth, gonad function, and plumage pattern and growth rates in 98 complete and 154 incomplete thyroidectomized Brown Leghorn roosters.

2. Development of the gonads and secondary sexual characters of adult, completely thyroidectomized roosters was markedly reduced. The greater degree of development of partial thyroidectomized males compared to complete operates became more conspicuous with increasing age.

In athyroidic fowl no spermatogenic stages beyond secondary spermatocyte were observed as late as 22 months of age. The vas deferens remained relatively thin and straight.

With androgen injections, a lesser comb growth was revealed in athyroidic fowl than in capons. The comb of capons and athyroidic males displayed a more

marked growth following the simultaneous administration of thyroxin and testosterone propionate than with either alone.

3. Following thyroidectomy, all plumage stages exhibited a replacement of normal pigmentation by reddish-brown pigment and a decrease in barbulation.

The male plumage pattern was produced in athyroidic roosters with an adequate dose of thyroxin without regard to testicular secretion.

The normal female plumage pattern was not produced by the administration of alpha-estradiol benzoate in thyroidectomized roosters, as is the case in normals. The female pattern appears to result from the synergistic action of thyroid and ovarian secretions.

The modifications of feather pattern conformed to the differences in thresholds of feather areas, as well as within individual feathers.

4. After thyroidectomy, the feather growth rates were reduced, but the growth of the posterior breast was most rapid for a longer period than the other areas, as in the normal.

The normal feather growth rates can be restored in thyroidectomized roosters by administration of thyroxin. A tract specificity appeared to exist as to the magnitude of stimulation obtainable by thyroxin administration, which corresponded closely to the normal feather growth rates.

The increase in feather growth rates following estradiol administration was accompanied by a tendency for the equalization of their absolute rates, as prevails in the normal hen.

5. Suggestions concerning the influence of the thyroid-pituitary-gonad interrelations on body growth, gonad function, and secondary sexual characters are discussed.

LITERATURE CITED

- ALLEE, W. C.; COLLIAS, N.; and LUTHERMAN, C. Z. 1939. Modification of the social order in flocks of hens by the injection of testosterone propionate. *Physiol. Zool.*, **12**:412-40.
- The American Standard of Perfection. 1938. Davenport, Iowa: American Poultry Association, Inc.
- ARON, M., and BENOIT, J. 1934. Sur le conditionnement hormonal du développement testiculaire, chez les oiseaux: rôle de la thyroïde. *Compt. rend. Soc. biol.*, **116**:218-21.
- BENOIT, J. 1923*a*. Transformation expérimentale du sexe par ovariectomie précoce chez la poule domestique. *Compt. rend. Acad. sci.*, **177**:1074-76.
- . 1923*b*. A propos du changement expérimental du sexe par ovariectomie, chez la poule. *Compt. rend. Soc. biol.*, **89**:1326-28.
- . 1935. Rôle de l'hypophyse dans l'action stimulante de la lumière sur le développement testiculaire chez le canard. *Ibid.*, **118**:672-74.
- . 1936. Rôle de la thyroïde dans la gonadostimulation par la lumière artificielle chez le canard domestique. *Ibid.*, **123**:243-46.
- . 1937. Thyroïde et croissance testiculaire chez le canard domestique. *Ibid.*, **125**:459-60.
- BENOIT, J., and ARON, M. 1934. Sur le conditionnement hormonal du développement testiculaire, chez les oiseaux: résultats de la thyroïdectomie, chez le coq et le canard. *Compt. rend. Soc. biol.*, **116**:221-23.
- BENOZZI, M. 1932. Appunti sulla istofisiologia della ghiandola tiroide embrionale (The histophysiology of the embryonic thyroid gland). *Arch. ital. anat. e embriol.*, **30**:452-68.
- BLIVAIS, B. B., and DOMM, L. V. 1941. Relation of thyroid gland to plumage pattern in the brown Leghorn fowl. *Anat. Rec., Suppl.*, **82**:458.
- . 1942*a*. Relation of thyroid gland to plumage pattern and gonad function in the brown Leghorn male. *Ibid.*, *Suppl.*, **84**:79.
- . 1942*b*. Relation of thyroid gland to plumage pattern and gonad function in the brown Leghorn female. *Ibid.*, p. 80.
- . 1944. Feather growth rates in thyroidectomized brown Leghorn fowl. *Ibid.*, *Suppl.*, **89**:37.
- BODANSKY, M. 1938. Introduction to physiological chemistry. 4th ed. New York: John Wiley & Sons, Inc.
- BOHREN, B. B.; CONRAD, R. M.; and WARREN, D. C. 1943. A chemical and histological study of the feather pigment of the domestic fowl. *Amer. Nat.*, **77**:481-518.
- BUCHANAN, G. 1926. The testis and thyroid in a hen feathered silver grey Dorking cock. *Brit. Jour. Exper. Biol.*, **4**:73-80.
- CARDROIT, F., and REGNIER, V. 1944. Effets de la thyroïdectomie sur l'ergot du coq adulte. *Compt. rend. Soc. biol.*, **138**:484-86.
- CHAUDHURI, A. C. 1928. The iodine content of the thyroid of the fowl with reference to age and sex. *Brit. Jour. Exper. Biol.*, **5**:366-70.
- COLE, L. J., and HUTT, F. B. 1928. Further experiments in feeding thyroid to fowls. *Poultry Sci.*, **7**:60-66.
- COLE, L. J., and REID, D. H. 1924. The effect of feeding thyroid on the plumage of the fowl. *Jour. Agr. Res.*, **29**:285-87.
- CREW, F. A. E. 1925. Rejuvenation of the aged fowl through thyroid medication. *Proc. Roy. Soc. Edinburgh*, **45**:252-60.
- DANFORTH, C. H. 1937. Pigment cells in heterogeneous feather. *Anat. Rec.*, **68**:461-68.
- DAVIS, D. E., and DOMM, L. V. 1941. The sexual behavior of hormonally treated domestic fowl. *Proc. Soc. Exper. Biol. and Med.*, **48**:667-69.
- DOMM, L. V. 1927. New experiments on ovariectomy and the problem of sex inversion in the fowl. *Jour. Exper. Zool.*, **48**:31-171.
- . 1929*a*. The effects of bilateral ovariectomy in the brown Leghorn fowl. *Biol. Bull.*, **56**:459-97.
- . 1929*b*. Some effects of hyperthyroidism in the brown Leghorn fowl. *Anat. Rec., Suppl.*, **44**:227.
- . 1937. Observations concerning anterior pituitary-gonadal interrelations in the fowl. Cold Spring Harbor Symp. Quant. Biol., **5**:241-57.
- . 1939. In: E. ALLEN (ed.), Sex and internal secretions, chap. v, pp. 227-327. 2d ed. Baltimore: Williams & Wilkins Co.
- DOMM, L. V., and BLIVAIS, B. B. 1944. Modifications in feather pattern and growth rate following administration of thiouracil in brown Leghorn fowl. *Proc. Soc. Exper. Biol. and Med.*, **57**:336-37.
- . 1946. Modifications in feather pattern and growth rate following thiouracil medication in the domestic fowl. *Anat. Rec., Suppl.*, **94**:68.
- DOMM, L. V.; DAVIS, D. E.; and BLIVAIS, B. B. 1942. Mating behavior in brown Leghorn fowl following sex hormone administration. *Anat. Rec., Suppl.*, **84**:31.
- DOMM, L. V., and GUSTAVSON, R. G. 1929. The effect of female hormone on plumage and oviduct of bilaterally ovariectomized fowl. *Anat. Rec., Suppl.*, **44**:228.
- DORRIS, F. 1939. The production of pigment by chick neural crest in grafts to 3-day limb bud. *Jour. Exper. Zool.*, **80**:315-45.
- EMMENS, C. W., and PARKES, A. S. 1940. The endocrine system and plumage types. II. The effects of thyroxine injections to normal, caponized, and thyroidectomized-caponized birds. *Jour. Genet.*, **39**:486-92.
- EVANS, H. M., and SIMPSON, M. E. 1930. Some effects on the hypophysis of hyper- and hypothyroidism. *Anat. Rec., Suppl.*, **45**:215.
- EVANS, H. M., SIMPSON, M. E., and PENCHARZ,

- R. E. 1939. Relation between growth promoting effects of pituitary and thyroid hormone. *Endocrinology*, **25**:175-82.
- FAULKNER, G. H. 1932. Observations on physiological factors in influencing the genetic coloration of fowl plumage. *Arch. Entw'mech. u. Org.* **126**:663-73.
- FIGGE, F. H. J. 1940. Pigment metabolism studies: the regulation of tyrosinase melanin formation by oxidation-reduction systems. *Jour. Cell. and Comp. Physiol.*, **15**:233-47.
- FLOWER, C. F., and EVANS, H. M. 1924. The repair of dwarfism following thyroidectomy by the administration of anterior hypophyseal fluid. *Anat. Rec., Suppl.*, **29**:383.
- FOULKS, J. G. 1943. An analysis of the source of melanophores in regenerating feathers. *Physiol. Zool.*, **16**:351-80.
- FRAPS, R. M., and BURROWS, W. H. 1939. Plumage reactions to theelin in thyroidectomized fowl. *Proc. Seventh World's Poultry Cong. and Exposition*, pp. 106-9.
- GALLAGHER, T. F., and KOCH, F. C. 1929. The testicular hormone. *Jour. Biol. Chem.*, **84**:495-500.
- GIACOMINI, E., and TAIBELL, A. 1927. Plumage modifications caused by thyroid and particularly those presumably sexual in hyperthyroidized fowl. *Rend. sess. r. Acad. sci. rst. Bologna cl. sci. fis.*, **31**:81-100.
- GOODALE, H. D. 1916. Gonadectomy in relation to the secondary sexual characters of some domestic birds. *Carnegie Inst. Washington*, publ. 243.
- GRAY, J. C. 1930. The development, histology and endocrine functions of the compensatory right gonad of the hen. *Amer. Jour. Anat.*, **47**:217-59.
- GREENWOOD, A. W., and BLYTH, J. S. S. 1929. An experimental analysis of the plumage of the brown Leghorn fowl. *Proc. Roy. Soc. Edinburgh*, **49**:313-55.
- GREENWOOD, A. W., and CHU, J. P. 1939. On the relation between thyroid and sex gland functioning in the brown Leghorn fowl. *Quart. Jour. Exper. Physiol.*, **29**:111-19.
- HAMILTON, A. 1940. A study of the physiological properties of melanophores with special reference to their role in feather coloration. *Anat. Rec.*, **78**:525-47.
- . 1941. Influence of adrenal and sex hormones on the differentiation of melanophores in the chick. *Jour. Exper. Zool.*, **88**:275-305.
- HAMMETT, F. S. 1926. Studies on the thyroid apparatus. XXIX. The role of the thyroid apparatus in growth. *Amer. Jour. Physiol.*, **78**:69-91.
- HARDESTY, M. 1935. The effect of thyroxin upon the feather of the guinea fowl. *Jour. Exper. Zool.*, **71**:389-418.
- HILL, R. T., and PARKES, A. S. 1935a. Plumage changes in hypophysectomized fowls. *Proc. Roy. Soc., London, B*, **117**:202-9.
- . 1935b. Effect of replacement therapy on the gonads, accessory organs and secondary sexual characters of hypophysectomized fowls. *Ibid.*, **117**:210-18.
- HOSKINS, W. H., and KOCH, F. C. 1939. The inhibition of comb growth in cockerels and capons by estrone. *Endocrinology*, **25**:266-74.
- IRWIN, M. R.; REINEKE, E. P.; and TURNER, C. W. 1943. Effect of feeding thyroactive iodocasein on growth, feathering and weights of glands of young chicks. *Poultry Sci.*, **22**:374-80.
- JAAP, R. H. 1934. Pigmentation and growth rate in the gray breast feathers of adult mallard drakes. *Proc. Soc. Exper. Biol. and Med.*, **31**:630-34.
- JONES, D. G., and LAMOREUX, W. F. 1943. Estimation of the size of comb of live fowl. *Endocrinology*, **32**:356-60.
- JOHN, M., and BARNES, B. O. 1931. The feather germ as an indicator for thyroid preparations. *Amer. Jour. Physiol.*, **98**:463-66.
- JOHN, M.; FAULKNER, G. H.; and GUSTAVSON, R. G. 1931. The correlation of rates of growth and hormone threshold in the feathers of fowls. *Jour. Exper. Zool.*, **58**:69-111.
- JOHN, M., and GUSTAVSON, R. G. 1929. Effect of the female hormone upon the sex type of the feathers of brown Leghorns. *Anat. Rec., Suppl.*, **44**:204.
- . 1930. The production of female genital subsidiary characters and plumage sex characters by injection of human placental hormone in fowl. *Jour. Exper. Zool.*, **56**:31-61.
- KRIZENECKY, J. 1927. Athyroidisme chez un poule de race Leghorn dorée; remarque sur le rapport entre la thyroïde et le type sexuel chez les poules. *Compt. rend. Soc. biol.*, **97**:1749-52.
- LADEBECK, E. 1921. Die Farben einiger Hühner-rassen. *Zeitschr. f. induktive Abstam. u. Vererb.*, **30**:1-62.
- LANDAUER, W. 1929. Thyrogenous dwarfism (myxedema infantilis) in the domestic fowl. *Amer. Jour. Anat.*, **43**:1-43.
- LARIONOV, W. T. 1931. Weitere Versuche über den Einfluss der Schilddrüse auf die Regeneration des Gefieders bei Pyrrhula. *Arch. f. Entw'mech.*, **124**:54-65.
- LILLIE, F. R. 1936. The development of the chick. 2d ed. New York: Henry Holt & Co.
- . 1942. On the development of feathers. *Biol. Rev.*, **17**:247-66.
- LILLIE, F. R., and JOHN, M. 1932. The physiology of development of feathers. I. Growth rate and pattern in the individual feather. *Physiol. Zool.*, **51**:124-84.
- LILLIE, F. R., and WANG, H. 1940. Physiology of development of the feather. IV. The diurnal curve of growth in brown Leghorn fowl. *Proc. Nat. Acad. Sci.*, **26**:67-85.
- . 1941. Physiology of development of the feather. V. Experimental morphogenesis. *Physiol. Zool.*, **14**:103-35.
- MCGEE, L. C.; JOHN, M.; and DOMM, L. V. 1928. The development of secondary sex characters in

- capons by injections of extracts of bull testes. *Amer. Jour. Physiol.*, **87**:406-35.
- MARTIN, J. H. 1929. Effect of excessive doses of thyroid on the domestic fowl. *Biol. Bull.*, **56**: 357-70.
- MARVIN, H. C., and SMITH, G. C. 1943. Technique for thyroidectomy in the pigeon and the early effect of thyroid removal on heat production. *Endocrinology*, **32**:87-91.
- MILLER, D. S. 1938. Lack of refractoriness to prolonged thyrotropin administration in birds. *Proc. Soc. Exper. Biol. and Med.*, **38**:453-55.
- MITCHELL, H. H., and CARD, L. E. 1927. The basal heat production of cockerels, pullets, and capons, of different ages. *Proc. Third World's Poultry Cong.*, pp. 202-12.
- MITCHELL, J. B., JR. 1929. Experimental studies of the bird hypophysis. I. Effects of hypophysectomy in the brown Leghorn fowl. *Physiol. Zool.*, **2**:411-37.
- MOORE, C. R., and PRICE, D. 1932. Gonad hormone functions and the reciprocal influence between gonads and hypophysis, with its bearing on the problem of sex hormone antagonism. *Amer. Jour. Anat.*, **50**:13-71.
- NALBANDOV, A. N., and CARD, L. E. 1943. Effect of hypophysectomy on growing chicks. *Jour. Exper. Zool.*, **94**:387-414.
- NICKERSON, M. 1946. Relation between black and red melanin pigments in feathers. *Physiol. Zool.*, **19**:66-76.
- PARHON, C. F. 1924. Contribution à l'étude des suites de la thyroïdectomie chez des jeunes oiseaux et ses effets sur le croissence et le développement du plumage; infantilisme thyroïdien expérimentale. *Compt. rend. Soc. biol.*, **91**: 765-66.
- PARKES, A. S., and Selye, H. 1937. The endocrine system and plumage types. I. Some effects of hypothyroidism. *Jour. Genet.*, **34**:297-306.
- PAYNE, F. 1944. Anterior pituitary-thyroid relationship in the fowl. *Anat. Rec.*, **88**:337-53.
- RAPER, R. S. 1932. Tyrosinase. *Ergebn. Enzymforsch.*, **1**:270-79.
- RIDDLE, O. 1932. In: E. ALLEN (ed.), *Metabolism and sex*, chap. vi, pp. 246-80. 1st ed. Baltimore: Williams & Wilkins Co.
- RIDGWAY, R. 1912. *Color standards and nomenclature*. Washington, D.C.: The author.
- ROWAN, W. 1926. On photoperiodism, reproductive periodicity and the annual migration of birds and certain fishes. *Proc. Boston Soc. Nat. Hist.*, **38**:147-89.
- SALMON, T. N. 1936. Effect of thyro-parathyroidectomy in newborn rats. *Proc. Soc. Exper. Biol. and Med.*, **35**:489-91.
- SCHNEIDER, B. A. 1939. Effects of feeding thyroid substance. *Quart. Rev. Biol.*, **14**:289-305.
- SCHOOLEY, J. P. 1937. Pituitary in pigeon. *Cold Spring Harbor Symp. on Quant. Biol.*, **5**: 165-79.
- SCHWARZ, E. 1930. Pigmentierung, Form und Wachstum der Federn des Haushühns in Abhängigkeit von der Thyroideafunktion. *Arch. f. Entw'mech. Org.*, **123**:1-38.
- SCOW, R. O., and MARX, W. 1945. Response of pituitary growth hormone of rats thyroidectomized on the day of birth. *Anat. Rec.*, **91**:227-34.
- SIMMONS, E. L. 1943. A study of thyroid function in the white Leghorn capon and cockerel. Ph.D. Thesis. Contrib. No. 329. Indiana University, Department of Zoology.
- SMELSER, G. K. 1934. Effect of thyroidectomy on testicular function. *Anat. Rec., Suppl.*, **80**:53.
- . 1939. The effect of thyroidectomy on the reproductive system and hypophysis of the adult male rat. *Ibid.*, **74**:7-16.
- SMITH, P. E. 1933. Increased skeletal effects in A.P. growth hormone injections by administration of thyroid in hypophysectomized, thyro-parathyroidectomized rats. *Proc. Soc. Exper. Biol. and Med.*, **30**:1252-54.
- 'STUDENT.' 1925. New tables for testing the significance of observations.
- THOMPSON, W. O. 1942. In: *Glandular physiology and therapy*, chap. xxv, pp. 413-42. Chicago: Amer. Med. Assoc.
- TORREY, H. G., and HORNING, B. 1922. Hen-feathering induced in male fowl by feeding thyroid. *Proc. Soc. Exper. Biol. and Med.*, **19**:275-79.
- . 1925a. The effect of thyroid feeding on the moulting process and feather structure of the domestic fowl. *Biol. Bull.*, **49**:275-87.
- . 1925b. Thyroid feeding and secondary sex characters in Rhode Island Red chicks. *Ibid.*, **49**:365-74.
- VAN DYKE, H. B., and CH'EN, G. 1933. Production of ovulation by anterior lobe of pituitary of thyroidectomized rabbits. *Proc. Soc. Exper. Biol. and Med.*, **31**:327-28.
- WANG, H. 1943. The morphogenetic functions of the epidermal and dermal components of the papilla in feather regeneration. *Physiol. Zool.*, **16**:325-50.
- . 1945. Experimental alteration of growth rate in chimaeric feathers of breast-saddle origin in the brown Leghorn capon. *Ibid.*, **18**:335-64.
- WATERSON, R. L. 1942. The morphogenesis of down feathers, with special reference to the developmental history of melanophores. *Physiol. Zool.*, **15**:234-59.
- WILLIER, B. H. 1942. Hormonal control of embryonic differentiation in birds. *Cold Springs Harbor Symp. Quant. Biol.*, **10**:135-44.
- WILLIER, B. H., and RAWLES, M. E. 1944. Genotypic control of feather color pattern as demonstrated by the effects of a sex-linked gene upon the melanophores. *Genetics*, **29**:309-30.
- WINCHESTER, C. F. 1939. Influence of thyroid on egg production. *Endocrinology*, **24**:697-701.
- ZALESKY, M., and WELLS, L. J. 1937. Experimental studies of the thyroid. I. Effects of

thyroidectomy on reproductive organs in males of an annual-breeding ground squirrel. *Anat. Rec.*, **69**:79-97.

ZAWADOWSKY, B. M. 1925*a*. The effect of feeding fowls on thyroid gland. *Endocrinology*, **9**:125-36.
 ———. 1925*b*. The effect of single doses of thyroid gland on fowls. *Ibid.*, **9**:232-41.

ZAWADOWSKY, B. M., and ROCHLIN, M. 1928. Zur

Frage nach den Einfluss der Hyperthyroidisierung auf die Färbung und Geschlechtsstruktur des Hühnergefieders. *Arch. f. Entw.-mech.*, **113**:323-45.

ZAWADOWSKY, M. M. 1926. Bisexual nature of the hen and experimental hermaphroditism in hens. *Trans. Lab. Exper. Biol. Zoopark., Moscow*, **2**:164-94.

PLATE I

FIGS. 1-3.—Adult normal and thyroidectomized roosters.

FIG. 1.—Adult normal rooster, six months of age, shows well-developed comb and wattles which are red and turgid, and prominent ear lobes.

FIG. 2.—Adult complete thyroidectomized rooster (No. 5614) at 10 months of age. Thyroidectomy completed at 10 days of age. Note the smaller body, squatty stance, and the rugged appearance of the plumage compared to the normal. The comb and wattles are much reduced in size, pale and less turgid than in the normal. The ear lobes are also smaller.

FIG. 3.—Adult incomplete thyroidectomized rooster (No. 3440) at 10 months of age. Original thyroidectomy completed at 9 days of age. Note the reduced body size compared to the normal, though larger than the complete operate. This bird displays a squatty stance and rugged plumage. The plumage is generally

typical of thyroidectomy but also displays areas of normal pigment and form, especially at the tips and bases of individual feathers.

FIGS. 4-6.—Testes of adult fowl (magnifications: *a*, $\times 115$; *b*, $\times 650$).

FIG. 4.—Testes of adult normal Brown Leghorn (No. 1331), 6 months of age, showing tubules in full spermatogenesis.

FIG. 5.—Testes of adult thyroidectomized Brown Leghorn (No. 1471), 6 months of age, showing primordial germ cells and primary and secondary spermatocytes. Note compact arrangement of tubular and intra-tubular cells, typical of an immature testis.

FIG. 6.—Testis of adult thyroidectomized Brown Leghorn (No. 1362), 22 months of age, showing primary and secondary spermatocytes but no mature spermatozoa. Note compact arrangement of tubules and intra-tubular tissue.

PLATE II

FIGS. 7-12.—Types of homologous adult normal and thyroidectomized rooster feathers; in each pair, normal to left and thyroidectomized to right. Fig. 7, posterior breast; Fig. 8, neck hackle; Fig. 9, saddle; Fig. 10, wing coverts; Fig. 11, primary flights; Fig. 12, secondary flights.

FIGS. 13-15.—Photographs of feathers of adult thyroidectomized roosters after adminis-

tration of thyroxin. (In all figures, *a*, posterior breast; *b*, anterior breast; *c*, back; and *d*, saddle.) Note the athyroidic condition of the feather tips in Figs. 13 and 14.

FIG. 13.—Injection of 0.1 mg. thyroxin on day 24 or 32 after feather plucking. Observe deposition of black melanin for a longer period in saddle than in other areas and the greater area of barbulation than pigment deposition.

PLATE III

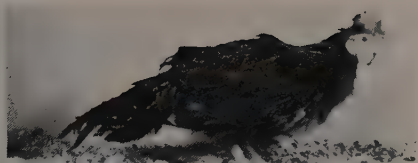
FIG. 14.—Four injections of 0.1 mg. thyroxin at 6-day intervals, starting on day 22. The part of the feather developed after the second or third injection is typical of a normal rooster as to color and form. Observe persistence of a single dose for at least 6 days.

FIG. 15.—Alternate-day injection of 0.05 mg. thyroxin from second to thirtieth days. Posterior and anterior breast feathers are normal in appearance. Back and saddle have barbulation and melanin deposition in excess of normal.

PLATE I



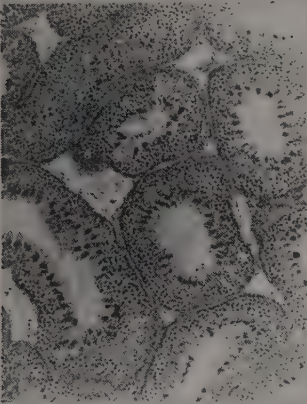
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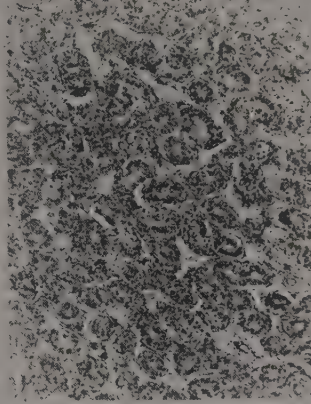
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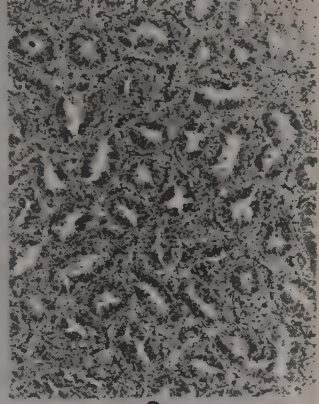
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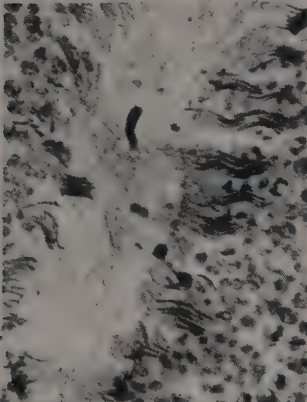
4a



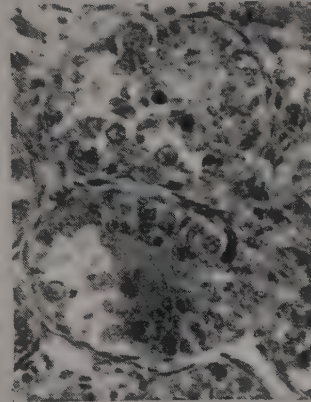
5a



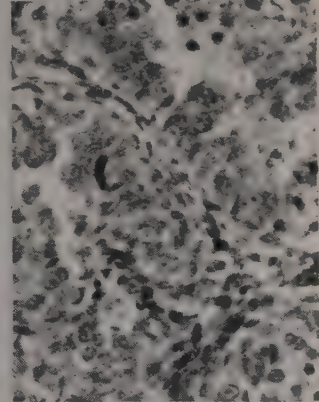
6a



b



b



b

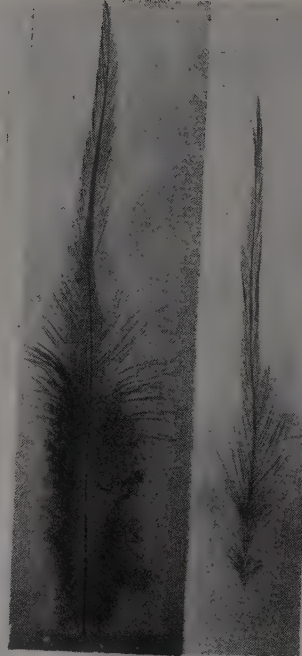
PLATE II



7



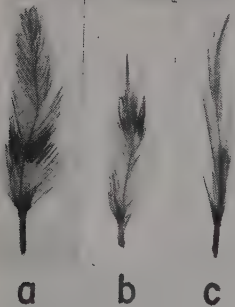
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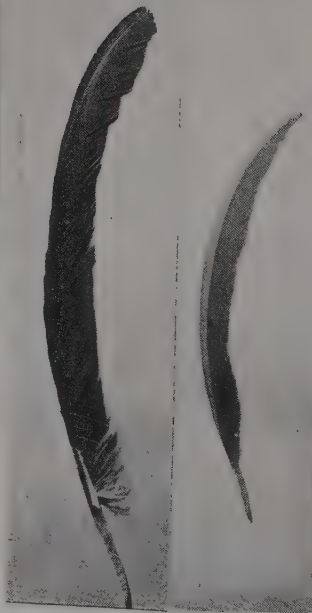


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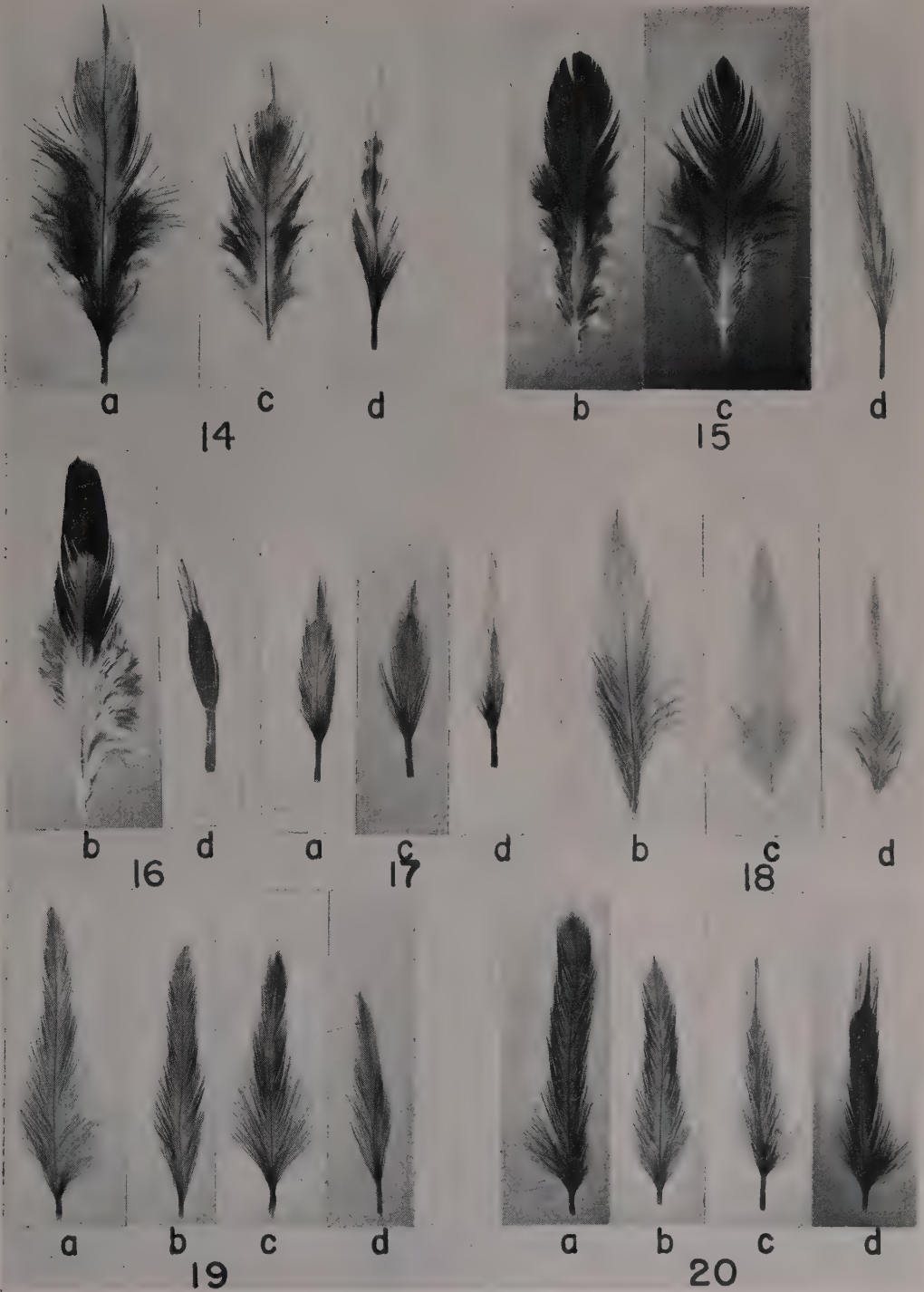


11



12

PLATE III



FIGS. 16-20.—Photographs of feathers of adult normal and thyroidectomized roosters after administration of alpha-estradiol benzoate. (In all figures, *a*, posterior breast; *b*, anterior breast; *c*, back; *d*, saddle.) Note the athyroidic condition of the feather tips in Figs. 17-20.

FIG. 16.—Daily administration to normal rooster of 13 γ of estradiol for 2 days, starting on day 14. Salmon-colored area develops in breast, and mottled dark brown and broad webbed area forms in back and saddle.

FIG. 17.—In athyroidic rooster, daily administration of 30 γ of estradiol for 15 days, starting on day 18 or 22. Breast shows slight broadening of web. Saddle shows broadening of web and deposition of black melanin in a mottled pattern.

FIG. 18.—Daily administration in an ath-

thyroidic rooster of 109 γ of estradiol for 20 days, starting on day of plucking or 4 days later. Breast feathers show a broadening of vane and web and a deposition of black melanin in a mottled pattern. Back displays a broader vane and web and a mottled deposition of black and brown melanin.

FIG. 19.—Daily administration in an athyroidic rooster of 194 γ for 22 days, starting on day of plucking or 4 days later. All areas show a broadening of web and vane and deposition of black and brown melanin in a mottled pattern.

FIG. 20.—Group I incompletely thyroidectomized rooster received 75 γ of estradiol daily for 8 days, starting on day 18, followed by 125 γ for 10 days. Greater degree of barbulation and black and brown melanin deposition in all areas than with larger doses in athyroidic roosters.

